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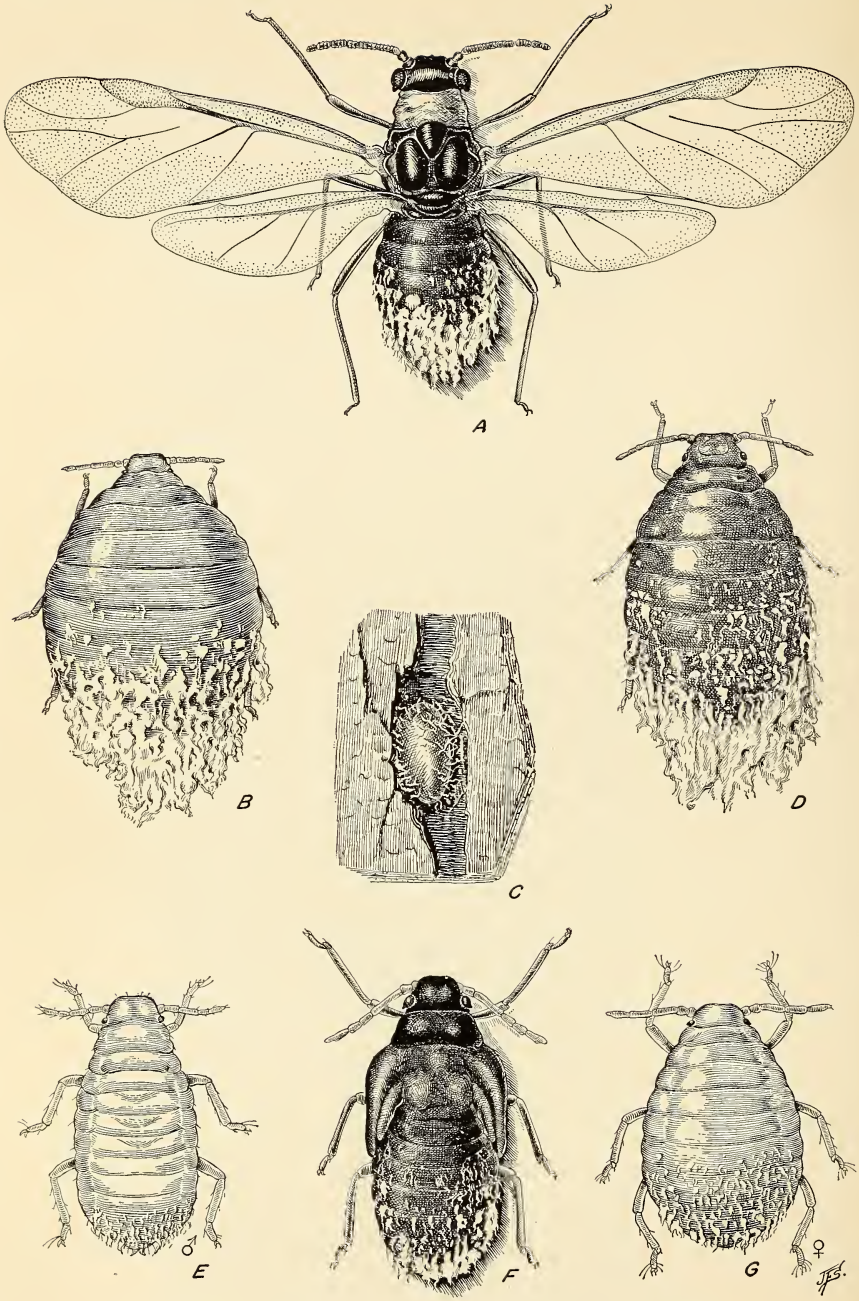

FORMS OF THE WOOLLY APPLE APHIS (ERIOSOMA LANIGERA).

A, Winged viviparous female, fall migrant; *B*, stem-mother; *C*, egg; *D*, wingless viviparous female, summer form; *E*, male; *F*, pupa of fall migrant; *G*, oviparous female. All much enlarged (Original.)

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THE WOOLLY APPLE APHIS.

BY

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THE WOOLLY APPLE APHIS.

By A. C. Baker, *Entomological Assistant, Deciduous Fruit Insect Investigations, Bureau of Entomology.*

INTRODUCTION.[1]

The woolly aphis, *Eriosoma lanigera* (Hausmann) (Pl. I), is without doubt one of the most troublesome and widely distributed apple pests. Its ravages have long been known. Even as early as 1832 the Académie de Rouen offered a gold medal for an essay, "Exposer l'Histoire naturelle du Puceron lanigère." This is sufficient evidence of the importance of the species at that time. It is now present in nearly every region of the globe in which the apple is grown, and the losses caused by it can scarcely be estimated. But notwithstanding the fact that the ravages of the "louse" are only too well known, its life history has remained little understood. The writer was, therefore, in January, 1912, instructed to make a detailed study of the species.

Experiments were begun in the spring of 1912 along a number of possible lines. The forms upon elm suggested themselves on account of their structural similarity to one another. Experiments, using elm, apple, and *Ribes*, were therefore started. *Ribes* was used because it is known that *Eriosoma ulmi* Linnæus in Europe migrates to this food plant, and biological proof was desired to back up the structural separation of that species from others. All the experiments with *Ribes* proved negative, as would be expected, and therefore they were not continued during the season of 1913.

While these experiments were under way, two brief notes were published. One, by Gillette (1912), announced the finding of fall migrants of *lanigera* on elm. The other, by Miss Patch (1912a), gave the results of her experiments in transferring from elm to apple the species which she considered *Eriosoma americana*. The writer's experiments did not agree with hers, since that which he considered *americana* would not feed upon apple, but they did agree in that the elm was proven to be the winter host of *lanigera*. To Miss Patch therefore is undoubtedly due the credit for first having placed before the public the fact that the woolly aphis migrates from the elm to the apple in the spring and in the fall returns to the elm. That the writer, without knowing of her experiments, ascertained the same fact only goes to strengthen her observations.

[1] Figures in parentheses refer to "Literature referred to in the text," pages 53–55.

When the experiments with *Ribes* proved negative, it was evident that three species were present on elms, namely, *ulmi*, *americana*, and *lanigera*. It was hoped that by means of collections of spring migrants from different localities throughout America the ranges of these species could be definitely known. Such extensive collections it was found impossible to obtain, and the idea of mapping the different species in connection with the present study was abandoned. Many entomologists, however, sent material, and to all of these the writer is indebted. J. J. Davis also sent his microscope slides of *ulmi* from Europe, and the writer was thus able to see specimens of that species from different regions.

In the detail work of the experiments the writer was ably assisted during the season of 1912 by Mr. James Luckett, and in working up the literature he was kindly helped by Messrs. H. P. Gould and R. A. Cushman. Finally, whatever value the present study may have, much of it is due to Prof. A. L. Quaintance, who not only placed in the writer's hands many interesting notes on the species, but gave him every facility for conducting his investigations.

The writer has endeavored herein to be brief, to give summaries rather than totalities and results rather than experiments. A somewhat detailed study of the structure of the species has been attempted. This, it is hoped, will serve as a basis for future work on other members of the family.

EARLY HISTORY.

The earliest European account of this insect seems to be the original description by Hausmann in 1802. It was next discussed by J. Banks in a paper read in 1815 and printed in 1817. In connection with this paper a plate depicting the insect was published. Contrary to the general rule with early accounts, this plate is fairly accurate, and for its historic interest it is here in part reproduced. (Pl. II.) In 1816 Salisbury gave an account of the insect and figured what he supposed to be the egg. This writer held it to be indigenous to Europe, but his grounds for so doing seem not very strong, for he bases his conclusion upon statements of his gardener, and he himself confused several species. Kirby and Spence (1815) state definitely that the insect was not known in England until 1787 and that it was traced by Banks to a nursery in Sloan Street and had probably been introduced from America. It must, however, judging from Banks's remarks, have been well known in England by 1794. Amyot and Serville (1843) give Tourgard as authority for the statement that the insect first appeared in France in 1812 and in Belgium in 1829. Of French writers, Blot and De Longchamps, on the other hand, believed the insect indigenous. It has in late years been studied in all the important European countries.

In the United States no very early records occur. This is hardly to be wondered at considering the status of entomology in the early days. No doubt the "louse" was well known here before anyone would venture to lower his dignity by referring to it. The following reference in the Domestic Encyclopedia (1803) may apply to this insect:

> Blight-insects (Aphides or plant-lice), may be destroyed by the smoke of tobacco, or by scattering on them Scotch snuff. Another method, is to place a few of the larvae of beetles, called ladybirds, or Lady-cows (*Coccinellæ septem-punctatæ*) on the plants infested with the blites, which, it is asserted, will be thus in a short time destroyed.

In 1817 Coxe in his "Cultivation of Fruits"[1] states that white-washing the trunks "destroys many kinds of lice injurious to fruit trees," but he describes none of them. The aphis was discussed by J. Buel in 1836 under the name *Aphis lanata*, and a somewhat complete account was given by Harris in 1842. In cultural manuals it was described by Kenrick in his "New American Orchadist" (1844), by Downing in "Fruit and Fruit Trees" (1845), and by Thomas in "Fruit Culturist" (1846). It was considered also by early entomologists, such as Fitch, as will be noted under the specific name.

In Canada it was reported in 1856 from Nova Scotia (J. H. H., 1856), and in 1871 Bethune gave an account of the species in Ontario. It is interesting to note that in the files of the Bureau of Entomology there is a communication dated London, Ont., Aug. 20, 1876, in which *lanigera* is recorded from *Cratægus*. This is possibly one of the earliest observations on the interesting habit recently so well pointed out by Miss Patch (1912).

In the South the insect has been observed and studied in Mexico by Inda. It is also abundant in Brazil, and Rivera reports it as very troublesome in Chile.

In South Africa, according to Mr. C. P. Lounsbury, this aphis is one of the most troublesome of apple pests, being distributed throughout Cape Colony. In Natal, too, it is abundant and, to quote Fuller (1904), "is found all over the country, and is certainly the worst of all the pests—insects or fungi, attacking this favorite fruit." It is also reported by Mr. C. W. Howard to be injurious in the Transvaal.

In Australia the work of Messrs. T. Lang and Co. in 1868–70 was the beginning of the commercial application of aphis-resistant stock. Such an undertaking by a commercial firm argues for a very early introduction. In America the Australian work was reviewed in the California Horticulturist (1872) and in 1874 Mackay discussed the ravages of the insects in Australia, New Zealand, and Tasmania.

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[1] Coxe, William. A View of the Cultivation of Fruit Trees and the Management of Orchards and Cider . . . p. 38. Philadelphia, November, 1817.

The first record given by Atkinson in India is 1889, but when an insect such as the woolly aphis "has destroyed nearly every orchard in Conoor" it has undoubtedly long been a resident.

Recently this same insect has been discussed at length in Japanese (The Insect World, 1909). The author of that article, in giving its history, credited *Aphis lanigera* to Hausmann, but in treating the genus *Eriosoma* wrote it *Eliosoma*. No references to the species have been found in Chinese literature, but without doubt it exists in that country.

It will be seen, then, that the woolly aphis is distributed over practically the entire apple growing regions of the world, and the question naturally arises, Whence did it come? It is difficult at this late date to ascertain with certainty the home of such an insect. So far as the evidence goes, it would seem, however, to be of American origin. This conclusion is based upon the following facts:

1. Tradition recounts the importation of the species into Europe from America.
2. The primary host of the species is the American elm.
3. The summer generations occur in this country upon crab apples, mountain ash, and *Cratægus*—all native trees.
4. The spring migrants must be rare in Europe, judging from published accounts of elm insects.
5. In spite of its conspicuous character the insect is not discussed in the older European horticultural works.

The writer considers the species to have been originally an elm-*Cratægus* feeder which later adopted the apple. This he believes because of the widespread, though not abundant, occurrence of the insect on these two trees in their native home. Throughout the limestone regions *lanigera* has been present on the thorns for many years. That it was not recorded on these trees until the early seventies is, he believes, because the fact was not considered worthy of note. Moreover, in the north he has seen the insect on *Cratægus* so far removed from orchard trees that there could have been no flight between the two. It is then his firm belief that the original home of *Eriosoma lanigera* was throughout the great limestone regions of temperate America. When these regions were planted to apple the aphis adopted these trees as its secondary host, and by means thereof has spread throughout the world. Its habits have been altered to suit both host and climate in many countries, but in its native home it still continues its regular cycle of alternation.

SEXES AND EGGS.

The earliest account of the ovipara of this species and of the egg is, to the best of the writer's knowledge, the following, by L. O. Howard (1880):

The winter egg was found on several occasions during the winter in crevices of the bark over which a colony had been stationed during the summer. It

was a rather long ovoid, measuring .322^{mm} (.125 inch) in length and was very similar to the winter egg of *Colopha ulmicola* (Fitch), as described by Riley in Bulletin No. I, Vol. V, Hayden's Survey.

This egg was laid, as Professor Thomas supposes, by a wingless female, differing from the ordinary agamic form to a certain extent. These females we only know from finding their skins around the winter egg, since they often die without depositing it. The males we have not seen.

The first complete account of the sexual forms seems to have been that of Goethe (1883). He gave figures of both male and female. Numerous other accounts appeared from time to time. Of these one of the most interesting is that of Lignières in 1895. This writer describes the courtship of the species, and from our observations at Vienna, Va., the males still retain the customs of their forefathers. Alwood's account in 1904 appears to be the first full American publication on the sexes, and since that date many descriptions, more or less complete, have appeared. It should be noted that the so-called male figured by Buckton in his monograph is nothing but a first-instar wingless viviparous female.

NAME.

GENERIC NAME.

In the original description of the species *lanigera* was placed under the genus *Aphis*. In 1820 Leach characterized the genus *Eriosoma* in a footnote in connection with a paper read by Mosley before the Horticultural Society of London. The paper was read in 1817 and published in 1818. The genus was characterized as follows:

Eriosoma has its body covered by woolly matter; its abdomen has neither horns nor tubercles, and its antennæ are short. The body of Aphis is naked, its antennæ are long and setaceous, and the abdomen is furnished with a tubercle, or horn-like process on each side.

The genus was erected for "Latreille's third division of the genus *Aphis*," and the *Aphis lanigera* of Hausmann is indicated as type. Previously what is supposed to be this species was cited as *Coccus mali* by Bingley (1803).

In 1819 Samouelle published his "Entomologist's Useful Compendium," and on page 232 characterized the genus "*Eriosoma*—Leach's MSS." It seems evident that the printed copy of the Society's Transactions had not reached Samouelle when his book went to press, but "Leach's MSS." is evidence of the fact that he knew that the characterization of the genus would shortly be published. The obscurity of the generic description in the Transactions has led to the crediting of the genus to Samouelle. Some recent writers also have used *mali* as the specific name, following Samouelle, who, in this connection, substituted it for *lanigera*, no doubt from knowing "Leach's MSS."

Seemingly without knowledge of either of the generic descriptions just mentioned, Blot, in a paper read in 1823 and published in 1824, described the genus *Myzoxyle* for the apple "louse," as follows:

Genre nouveau détaché du genre *Puceron*, et auquel l'auteur donne pour charactères distinctifs des antennes de cinq articles renflés, dont le second est le plus long, et le troisième est le plus court; point de tubercules ni de cornes à l'anus; des tarses de deux articles, et deux crochets accolés, difficiles à distinguer. Le nom *Myzoxyle* vient de deux mots grecs, qui signifient suce-bois.

This spelling was changed to *Myzoxylus* in 1831, and *mali* was used as specific. Another variation of the same word was *Myzoxile*, used by Avrilly in 1834. It was not until 1841 that Hartig erected his genus *Schizoneura*, which has for some years been the name used in connection with *lanigera*. It would seem that Hartig was in doubt about the name *lanigera*, for it was written thus: "*Schiz. lanigera* Banks?"

From the foregoing there seems little doubt that *Eriosoma* is the generic name which should be used for this species and that the synonymy of the genus will stand as follows:

Eriosoma Leach, 1818.
Eriosoma Samouelle, 1819.
Myzoxyle[1] Blot, 1824.
Myzoxylus Blot, 1831.
Myzoxyle[1] Avrilly, 1834.
Schizoneura Hartig, 1841.

SPECIFIC NAME.

The woolly aphis was first described by Hausmann (1802) under the name of *Aphis lanigera*, as follows:

APHIS LANIGERA.

I. Blattlaus der ersten Generazion. Länge eine, Breite eine halbe Lin. Der Körper eiförmig und stark gewölbt. Kopf, Augen, Fühlhorner, Saugrüssel, und Schenkel haben eine schwärzliche, Halsschild und Hinterleib eine dunkel honiggelbe Farbe und Glanz. Der Hinterleib überall mit einer zarten, weisslichen, ins Bläuliche sich ziehenden, flokkigen Wolle bedekkt, die oft zwei bis dreimal die Länge des Körpers übersteigt. Fühlhörner, Beine und Saugrüssel sind im Verhältnisse zur Grösse des Körpers sehr kurz. Die Hörner auf dem Rükken fehlen dieser Art.

II. Vollkommne Blattlaus der zweiten Generazion. Flügellos; etwas kleiner und schmaler als die Blattlaus der ersten Generazion; im Uebrigen ihr gleich.

III. Unvollkommne Blattlaus der zweiten Generazion. Von den vollkommne nur durch die geringe Grösse und hellere Farbe des Körpers unterschieden.

Aphis lanigera nährt sich von dem Safte der Borke und des Splints der Apfelbäume. Da sie in grossen Haufen nebeneinander lebt, so bekommt die Borke der zarten Zweige durch die vielen Stiche ihres Rüssels das Ansehn eines feinen Zellgewebes. Bei grössern Zweigen, deren Borke härter ist, sucht

[1] Without standing.

sie sich unter diese zu arbeiten, um aus dem darunter liegenden Splinte, in welchen sie ihre Saugrüssel leichter einsenken kann, Nahrung zu ziehen. Zuweilen bringt sie an den Zweigen sogar Auswüchse hervor, in dem der Reiz, den sie durch ihre Stiche verursacht, einen stärkern Zufluss der Säfte nach einer Stelle, bewirkt.—Diese Blattlaus giebt, wie *Aphis bursaria*, einen weisslichen, gummiartigen Saft von sich. der sich oft zu Tropfen von i Linie im Durchmesser anhäuft.

One year later, according to Atkinson, Bingley discussed the species under the name *Coccus mali*. In 1820 Leach, in connection with his generic description, displaced *lanigera* in a most convenient manner, as follows:

Since all the Eriosomata, as their name imports, have their bodies covered by woolly matter, the term *lanigera* is objectionable in a specific sense. The name *Mali* might therefore be substituted for it, and as this species occurs principally on the *Pyrus malus*, I therefore propose to call it *Eriosoma Mali*.

He was in this apparently followed by Samouelle, who discarded "the *lanigera* of authors" for *mali*. The French writers apparently also followed Leach in using *mali*, but in 1841 Hartig returned to *lanigera*, crediting the name, however, to Banks.

The *Pemphigus americanus* of Walker (1852) has been placed as a synonym of *lanigera*, but the writer can find nothing in the description which would confirm this, and Walker lists several species of *Schizoneura*. With Fitch's *Pemphigus pyri*, however, the case is different, and there is scarcely any reasonable doubt that the insect he had was *lanigera*. For some time Riley was of the opinion that our form and the European were distinct, and this led him to retain Fitch's *pyri*, though he considered it an *Eriosoma*. Very recently Woodworth (1913) has issued a publication on the woolly aphis, under the name *Schizoneura ulmi* L., but this is an evident error. The synonymy of the species will stand as follows:

Eriosoma lanigera (Hausmann).
Aphis lanigera Hausmann, 1802.
Coccus mali Bingley, 1803.
Eriosoma mali Leach, 1818.
Eriosoma mali Samouelle, 1819.
Myzoxylus mali Blot, 1831.
Schizoneura lanigera Hartig, 1841.
Pemphigus pyri Fitch, 1856.
Eriosoma pyri Riley, 1869.
Schizoneura ulmi Woodworth, 1913.

Ulmi Linnæus: The European elm leaf-curl aphis is a very characteristic species which winters on the elms, forming a curl similar to that of our *americana*, and migrates to *Ribes* during the summer. The summer form was described as *fodiens* by Buckton. In studying our species on the elm, Riley, who had seen the European insect, separated ours therefrom under the name *americana*. Unfortunately in his description he did not go into sufficient detail in

regard to the antennæ to allow of separation on the description. This has led later writers here to doubt the validity of *americana*. In particular may be mentioned Gillette, who referred our form to *ulmi*. In her published work Miss Patch also seems inclined toward the same view, although she has informed me by letter that she considers the two distinct.[1] This condition of affairs has arisen, the writer believes, on account of the lack of European material in this country, and the presence here rarely of true *ulmi*. A glance at Plate III, *F–K*, will show a considerable difference between the two species in regard to spring migrants. The fall migrants, however, may be more easily confused, as the antennæ are of almost equal lengths. In *fodiens*, however, there is one character which easily separates it from *americana*. This is the presence of the large fringed sensoria on segments V and VI of the antennæ (Pl. III, *A*, *B*, and *C*). The writer has never seen a fringed sensorium of the fifth segment of *americana*, and those upon the sixth are all very small. The spring migrant of *ulmi* has the third segment of the antennæ as long as III–VI of the *americana* migrant, and this alone will separate the two species. There is, however, the same character of the sensoria noted in *fodiens*. The figures of Theobald (1912) would seem to indicate that his artist has confused two species in his drawings. *Ulmi* is correctly referred to in the text, but what seems to be *lanigera* is figured.

Americana Riley: In a recent note by Miss Patch (1912a) the specific name *americana* has been placed as a synonym of *lanigera*. To the writer there appears some doubt on this point, and sufficient evidence seems available to justify retention of the name, for the present at least. This evidence is of two kinds, structural and biological. In lots of elm aphides received in 1912 for migration tests there appeared two forms of migrants which were easily separated by the naked eye. The first of these was a large, rather long-legged form with thin antennæ. The other was smaller and more compact. Under the microscope the most marked difference was noted in the distal segment of the antennæ. The large forms all had a proportionately longer segment (Pl. IV, *C* and *E*), whereas those of the small form were short and thick (Pl. IV, *D* and *F*). Differences in the wings were also noted, as shown in Plate IV (*A*, large form; *B*, small form). This character, however, is not constant. These two forms were noted very plentifully at Vienna, Va., where the writer's experiments were conducted, and they were received from localities as far south as New Mexico and as far north as Michigan. It was noted that most of the large forms came from curled leaves of the elm, while most of the small ones were found in the rosettes. The

[1] Since the foregoing was written Miss Patch's note distinguishing the two species has been published (Patch, 1913).

insects were therefore separated into two lots, using only the naked eye, and the lots were placed separately upon apple twigs. The small forms began depositing young upon the apple in less than one minute, whereas none of the large forms deposited young, but all died. The writer was never able to rear the offspring of any of the large forms upon the apple, and all of the specimens collected from apple leaves in the spring had the characters of the small form.

There seems also to be a difference in the habits of the stem-mothers.[1] Those which produce the large forms are as a rule leaf-curl forms and appear later than those which produce the small form. These latter have been seen sitting at the base of a bud for 10 days and waiting for the leaves to grow and form a rosette around them. Taking all this into consideration the writer has thought best to restrict the name *lanigera* to those small forms, mostly from rosettes, which establish themselves on apple so readily, and to retain the name *americana* for the larger forms, which the writer has not been able to rear upon apple.

Cratægi Oestlund: A species of woolly aphis attacking *Cratægus* has been described under the foregoing name by Oestlund (1887). We have made no careful studies on this species recently, but collected it quite commonly in Ontario during 1909 and 1910. The fall migrants are very similar to those of *lanigera*, though our specimens are slightly larger. The antenna (Pl. III, *D* and *E*) is very close indeed to that of *lanigera*, and it is with difficulty that the two are separated. Measurements of a long series of specimens show that the relative lengths of the segments are not always constant. and though this character is the most reliable it can not always be depended upon. *Lanigera* occurs quite commonly upon *Cratægus*, and spring migrants from elms are found to establish themselves on that tree in the same manner as they do on the apple. The writer believes that a large series of reproduction experiments from the forms occurring in nature on *Cratægus* should be made before placing *cratægi* under *lanigera*. Such a series he has not been able to make; he therefore retains *cratægi*, although he believes it to be *lanigera*. The principal difference between this form and the woolly aphis is that segments V and VI of the antennæ of the migrant are longer in proportion.

Rileyi Thomas: There yet remains for discussion the species known as *rileyi* Thomas, the original *ulmi* of Riley. This name is generally applied to those forms making knotty growths on the twigs and trunk of the elm, the migrants of which are most commonly observed in the fall. These seem to be the summer and fall generations of a true elm species, which migrates to other elms in

[1] Since this paper was submitted Gillette has expressed this same opinion. (Gillette, 1912.)

the same way that *lanigera* migrates to the apple. It is true that spring migrants are also observed in the midst of colonies of *rileyi*, and these the writer believes come from sexes deposited in the old colonies by wingless females or fall migrants which, through inability or desire, fail to migrate. Hibernation also takes place in heavy colonies, and it is possible, therefore, that the cycles may overlap in point of time. The writer knows that this will happen with *lanigera*, as he has reared fall migrants of that species all winter in the greenhouses at Vienna, Va.

The migrations of the different species from elm are indicated in figure 1.

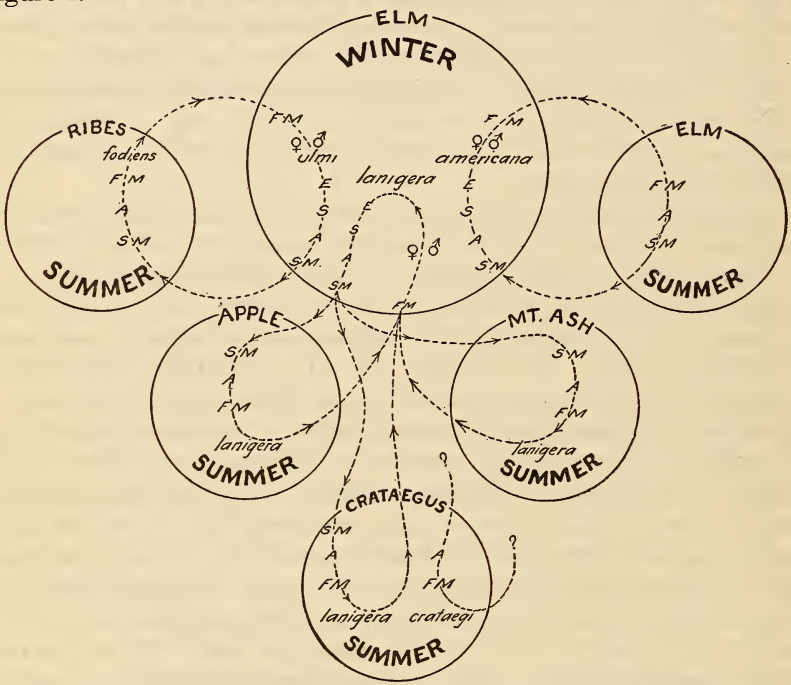

FIG. 1.—Life cycles of elm-feeding species of *Eriosoma: E*, egg; *S*, stem-mother; *A*, wingless viviparous female; *SM*, spring migrant; *FM*, fall migrant. (Original.)

Lanuginosa Hartig: This European species the writer has been unable to study. From Tullgren's (1909) figure of the antenna it would appear very close to some forms he has seen in this country. It is greatly to be regretted on this account that a study of the species could not have been made in connection with the others herein considered. Since specimens could not be obtained, the writer ventures here no opinion, merely pointing out the possibility that a study of the form might throw some light on the relations as we know them.

METHODS OF STUDY.

EXPERIMENTS.

It was found desirable, in studying the different forms of *Eriosoma lanigera*, to keep certain specimens under conditions similar to those met with on the roots. Various root cages were tried, but none of these seemed to give very good success. Finally the insects were kept in petri dishes partly filled with moist sand and allowed to feed upon fresh pieces of root. These pieces remained usable for two or three days. The petri dishes containing the feeding "lice" were stacked in racks, and these placed in a pit somewhat over 2 feet deep. In this way the "lice" were kept under almost soil conditions and did very well.

The aerial forms were grown on potted seedlings covered with lantern chimneys. One, two, and three year old trees were used, these being planted out and screened. Much difficulty was met with in rearing the leaf forms on elm. "Lice" which are partly grown appear to be unable to obtain food from leaves which are not curled. These forms died when placed upon even the most tender leaves and opening buds, but if transferred to another curled leaf they thrived very well. The method finally adopted in studying them was to locate curled leaves formed upon the trees under natural conditions, and after removing the occupants to place therein specimens of known lineage. The leaves were then tagged and observed at regular intervals. This method, however, entailed considerable labor, as it was necessary to do much climbing about in the trees in order to observe the insects. Nevertheless, it was the only method which gave satisfactory results, and such experiments were certainly under very nearly natural conditions.

The sexual forms were studied in life cells. These were made by gouging a small hole in a piece of cork and placing the insects therein. A cover slip was then cemented over the opening and the whole fastened to a small strip of wood. Pairs were placed in these cells for observation, and it was found in this way very easy to watch them under a binocular. The acts of molting, copulation, and egg laying were thus studied.

TECHNIQUE.

For description, specimens were mounted in the usual way in balsam, after being dehydrated and cleared. Sections were made by the ordinary methods adopted for such work. Killing and fixing was done with acetic alcohol, with sublimate. This was poured boiling over the living insects. It was found very difficult to use aqueous fixing solutions, as the aphides would not sink, and if any wax remained upon them it was found very difficult to wet them. Hence

acetic alcohol was used. Owing to the deep color of the insects, it was often necessary to bleach them in order properly to study certain structures. This was done by Mayer's chlorine method, using alcohol, which gave good satisfaction. For general views of the tracheal system the insects were plunged alive into acetic alcohol and examined at once. Dissections were made under the binocular in salt solution, glycerine, and clove oil. For the study of chitinous portions the insects were soaked in potassium hydroxide solution in the usual manner for several days.

FORMS OF THE SPECIES.

Counting the sexual egg as one stage and one form, *Eriosoma lanigera* occurs during its life cycle in forty-one different stages, seven generations, and eight distinct forms, as follows:[1]

Forms.	Stages.	Generations.
Egg	One	One.
Stem-mother	Five	
Spring wingless female	Five	One.
Spring migrant	Five	One.
Summer wingless female	Ten	Two.
Fall migrant	Five	One.
Oviparous female	Five	One.
Male	Five	
Eight	Forty-one	Seven.

The first four of these forms normally inhabit the elm. The spring migrant, summer wingless female, and fall migrant occur upon apple and related trees. The last three forms—fall migrant, oviparous female, and male—normally again take up their life upon the elm. There are, however, variations in this schedule of life which will be discussed elsewhere. Following are technical descriptions of the different forms whereby it is hoped that they may be separated from those of other and related species:

EGG.

(Pl. I, *C*.)

Size 0.64 mm. by 0.288 mm., elongate, elliptic, slightly curved, embedded in woolly secretion and covered with powdery white wax; when first laid, brown in color, but later turning to a dull purplish.

Location: Laid in the crevices of the bark of the elm tree; occasionally, but rarely, in similar positions on apple trees or in an old colony.

[1] The writer uses the word *form* to indicate any series of adult insects which are distinguishable by means of morphological characters, the egg being included only for convenience. The word *stage* he uses for any period of development of any form; thus the instars of all forms are stages. The word *generation* is used for any definite series of insects from their birth until their death.

STEM-MOTHER.

(Pl. I, *B*.)

Body yellowish or reddish and mottled over the dorsum with dusky or dark greenish, which sometimes gives the insect a greenish cast. Vertex and a patch upon the epicranium black or dusky. Antennæ with the two proximal segments dusky, the third yellowish, and the two distal ones black or nearly so. Rostrum dusky, with the exception of a band upon the labium, which is lighter. Anal plate dusky or black. Legs dusky, sometimes almost black.

The entire body is covered with a flocculent material, bluish-white in color. This is more pronounced on the caudal half of the abdomen, and there are especially long caudal tufts.

Morphological characters: Antennæ of five segments, with average lengths as follows: I, 0.048 mm.; II, 0.06 mm.; III, 0.144 mm.; IV, 0.064 mm.; V, 0.064 mm. Segment I is subcylindric and armed with a few prominent spine-like hairs; it is without imbrications. II is similar, but of a more even diameter. III cylindric, slightly enlarged distad, armed with a few prominent spine-like hairs and with faint indications of imbrication on the distal portion. There is also rarely indicated a small distal sensorium. Segment IV subcylindric, considerably enlarged distad, armed with several rather stout spine-like hairs and imbricated by a series of somewhat semicircular markings; these markings are composed of minute spine-like projections, placed close together so as to form rows. The segment is armed on its under distal extremity with a prominent fringed sensorium possessing an elevated, transparent central portion. Segment V subcylindric, armed with spines similar to those of segment IV and similarly imbricated. At about the distal fourth of the segment a group of sensoria is situated; these consist usually of one large and several smaller fringed sensoria. The distal extremity of the segment is armed with usually four or five prominent spines situated on tubercles. The vertex is almost straight and armed with small spines. The eyes are situated on tubercles, are black, and composed of three facets. The labium, which is composed of four segments, extends to the second pair of coxæ, rarely reaching beyond. Legs short, compared to the size of insect, the three pairs much alike, although those of the third pair are the longest. Dimensions of the hind leg as follows: Coxa, 0.112 mm. long, 0.108 mm. wide; femur, 0.336 mm.; tibia, 0.335 mm.; tarsus, proximal segment, 0.032 mm., distal segment, 0.086 mm. Cauda and anal plate rounded and very thickly set with prominent spine-like hairs. Cornicles, mere ring-like openings, very slightly elevated from the surface of the body. Length from vertex to tip of cauda, 2 mm. Form very globose, much more so than any of the future generations; abdomen crowded with embryos.

Location: Found at the base of the buds of the elm before the latter are open, or in the leaves of that tree that have opened and curled about them.

SPRING WINGLESS VIVIPAROUS FEMALE.

Body rusty or reddish brown, sometimes slightly purplish, rarely yellowish red or greenish red as is the stem-mother; dark markings, however, similar to those of the stem-mother. When placed in alcohol specimens of these turn a deep wine color, while stem-mothers usually show greenish red.

Body covered more or less with powdery bluish-white wax and with tufts of wax along the dorsum of the segments. These tufts are longer on the more caudal segments, where they often extend for a considerable distance beyond the body.

There is much variation in the size of this form.

Morphological characters: Antennæ of six segments with average lengths as follows: I, 0.033 mm.; II, 0.046 mm.; III, 0.128 mm.; IV, 0.048 mm.; V, 0.08 mm.; VI, 0.064 mm. Segment I subcylindric, armed with a few bristle-like hairs. II subpyriform, also with a few tubercled bristles. III subcylindric, slightly swollen at the distal extremity and with a few imbrications similar to those of the same segment of the stem-mother. IV subcylindric, slightly larger distad than proximad, armed with a few spines and with numerous semicircular imbrications, these formed by rows of minute setæ or projections as described in the stem-mother. V subcylindric, slightly enlarged distad, armed with a few spines, imbrications, and a circular, fringed, distal sensorium. This sensorium has a prominent central process or finger-like projection. VI subcylindric, with the distal fourth formed into a distinct unguis, at the base of which there is a prominent sensorial group. This is composed of one large sensorium with a central process and several small, circular, fringed sensoria. The segment is imbricated in the same manner as the distal segment of the stem-mother and on its distal extremity is armed with several stout spines situated on prominent tubercles. The vertex is straight and armed with numerous spines. The eye consists of a rounded tubercle, black in color, on which are three small circular lenses. The labium extends a slight way caudad of the third pair of coxæ. The legs are considerably longer in proportion than are those of the stem-mother, the segments of the hind leg being as follows: Femur and trochanter, 0.29 mm.; tibia, 0.33 mm.; tarsus, proximal segment, 0.03 mm., distal segment, 0.064 mm. Cauda and anal plate rounded and covered with numerous hairs; cornicles ringlike, more heavily chitinized mesad and cephalad, surrounded by several small spinelike hairs. Length from vertex to tip of cauda, 1.47 mm. Form more elongate than the stem-mother, but yet considerably swollen across the abdomen.

Location: Found upon the leaves of the elm, mostly in the so-called rosettes which the feeding of the insects causes to increase. Sometimes found in rolled leaves and sometimes numerous upon the twigs.

PUPA OF SPRING MIGRANT.

Body yellowish or reddish brown, often with purplish cast, dark markings when present faint; covered with a powdery bluish-white wax but not so flocculent as that of the apterous form and without long and prominent tufts of wax.

Morphological characters: Antennæ of six segments with proportional lengths as follows: I, 0.036 mm.; II, 0.048 mm.; III, 0.192 mm.; IV, 0.048 mm.; V, 0.08 mm.; VI, 0.08 mm. There is considerable variation in the lengths of the segments owing to the great difference in size between individuals. The relative lengths of the segments, however, seem fairly constant. Within the segments may be seen the nearly developed antennæ of the adult, the annulations of which are easily visible. The segments are armed with bristle-like hairs situated upon tubercles similar to those of the apterous forms, and the sixth segment is armed with a distal sensorium bearing a central process. At the base of the unguis of the seventh segment there is a sensorial group similar to that of the apterous female, and the segment is imbricated with semicircular markings composed of rows of minute seta-like projections. Such imbrications also sometimes occur upon the more proximal segments, and the antennæ are tipped with four or five stout bristles. The vertex is slightly depressed and is armed with stout bristles. The eyes are large and prominent, with the small eyes of the apterous forms remaining as tubercles on their caudal margin. Ocelli are present in their usual positions. The labium

extends nearly to the hind coxæ and the wing pads some distance caudad of them. Legs rather long and slender when compared with those of the apterous forms. Dimensions of hind leg as follows: Femur and trochanter, 0.32 mm.; tibia, 0.4 mm.; tarsus, proximal segment, 0.032 mm., distal segment, 0.11 mm. Cauda and anal plate rounded and covered with bristles. Length from vertex to tip of cauda, 1.22 mm.; length of wing pads, 0.51 mm.; width of abdomen at its widest diameter, 0.64 mm.; cornicles as in apterous female. Form rather elongate.

Location: Found in the spring upon the leaves and twigs of the elm, more commonly in rosettes, in company with spring apterous females.

SPRING MIGRANT.

General color reddish brown, wine colored, or slightly purplish. Appendages dusky to black; head, thoracic lobes, and sternal plate black; membranes between these, as well as the abdomen, brownish. Body covered with a bluish-white mealy wax, but with little flocculence, and rarely ever with the long strands of wax so common in the apterous female.

Morphological characters: Antennæ of six segments, sometimes of five, owing to the fusing of the third and fourth, the relative lengths as follows: I, 0.032 mm.; II, 0.048 mm.; III, 0.352 mm.; IV, 0.092 mm.; V, 0.092 mm.; VI, 0.08 mm.; unguis short and stubby. Segment I subcylindric; II subpyriform; III subcylindric, tapering proximad, where it is inserted in a cup-shaped depression in II. The segment is armed with a number of transverse sensoria, which vary greatly in number, the average being about nineteen. These appear as rings, but they extend only about half way around the segment, being, therefore, semicircular and arming the ventral surface of the segment. The dorsal surface is armed with a series of bristle-like hairs, situated upon tubercles. Segment IV is also subcylindric and is armed with five or six (the number varies considerably) sensoria similar to those on III. It is also armed above with bristle-like hairs as is that segment. Segment V subcylindric, somewhat enlarged distad. Like the more proximal segments it is armed with transverse sensoria upon its lower surface, the number varying, but four or five being the rule. On its upper surface it has a few stout bristle-like hairs on tubercles as have III and IV, but it also has more or less irregular transverse rows of minute seta-like projections which give it an imbricated appearance. The distal transverse sensorium is enlarged and club-shaped. It often, too, possesses an open irregular center which appears as if caused by the fusion of two sensoria. Segment VI subcylindric, rather stout proximad, armed with two or three transverse sensoria like those upon the other segments. The sensorium situated at the base of the unguis is much enlarged and very irregular, sometimes being plainly composed of two sensoria fused. In this region, also, there are a number of small, circular, fringed sensoria. At its distal extremity the segment is armed with several stout bristles, and a few more slender ones are situated more proximad. Imbrications similar to those upon V are present and very distinct. The unguis is in width about one-half that of the segment at its greatest diameter. Vertex straight or slightly depressed. Eyes with distinct ocular tubercles. Forewings transparent, with sometimes a slight clouding along the subcosta. Costa slightly curved; stigma greenish black, 0.416 mm. long on the costal margin, while the radial sector is 0.864 mm. long to its origin from the stigma; media obscured for some distance at its base, branching usually about half way between the origin of the cubitus and the tip of the wing measured along the media. Quite often the media is unbranched, being represented by one vein. Cubitus and anal vein arising quite

close together, about 0.076 mm. apart; width at greatest diameter of wing, 0.76 mm.; length at greatest length, 2.4 mm. Hind wing with the radial sector almost straight, the media curved, the cubitus almost straight, both cubitus and media fading at their bases. Width at greatest diameter, 0.48 mm.; length, 1.44 mm. Legs slender, dimensions of hind leg as follows: Femur and trochanter, 0.352 mm.; tibia, 0.704 mm.; tarsus, proximal segment, 0.032 mm., distal, 0.16 mm. Cornicle slightly elevated, ringlike, surrounded by hairs. Length from vertex to tip of cauda, 1.12 mm.

Location: Found in spring upon the leaves and twigs of the elm, in rosettes of leaves and occasionally in curled ones; also upon apple leaves and twigs, mostly upon the under surface of the leaves, depositing aptera. Those taken on apple at Vienna were secured mostly during the middle of May. On the elm they were noted much earlier and much later.

SUMMER WINGLESS VIVIPAROUS FEMALE.

(Pl. I, *D*.)

As between the different stages of any one form of this insect there is little of distinction except the size of the antennæ and the length of the labium. To save repetition, therefore, there are described of the other forms only adults and pupa. As a type, descriptions will be given of the stages of this most common form. The differences of antennæ, etc., found here, may be applied to other forms as well.

First instar.—When first born, pale reddish or yellowish brown, finally becoming dark brownish. The forms found in the early spring, and which have hibernated on the roots in this instar, are a dark greenish brown. In all forms the vertex and appendages are shaded with dusky, and indications of the same color may be noted about the spiracles. Eyes almost black. Born without any waxy covering, but this soon begins to show itself in the form of a bluish-white mealy secretion covering the entire body, with the exception of the appendages and the sutures. From the compound wax pores there is no distinct filamentous waxy secretion of any prominence excepting the "anal tufts," that which forms on the dorsum of the abdomen, being short and not well defined.

Morphological characters: Antennæ of five segments with average lengths as follows: I, 0.03 mm.; II, 0.024 mm.; III, 0.045 mm.; IV, 0.036 mm.; V, 0.045 mm. Sensoria are present on segments IV and V. The fifth segment is tipped with four prominent spines mounted on tubercles, and at the base of the unguis a group of sensoria is found. This consists of one prominent, oval, fringed sensorium which is always present, and one or two smaller, somewhat circular, fringed sensoria which may or may not be present. The central portion of the prominent sensorium is elevated to form a mushroom-like body, which proves to be a movable organ similar to that found in some species of *Phylloxera*. The central portions of the other sensoria are not elevated. The sensorium on IV is situated near the distal extremity of the segment, and is circular and fringed. The central portion is elevated, like that of segment V, but it forms, instead of a mushroom-like body, a simple cylinder or cone, which is also movable. Slightly proximad of this sensorium there is a very prominent spinelike curved hair situated on a tubercle. The hairs forming the fringe on all the sensoria are situated on small tubercles which are placed on a distinct rim. The vertex is straight and armed with a few setæ. The eyes are tuberculate and composed of three lenses. There are no ocelli. There is no suture immediately behind the eyes, but the first is situated as far caudad of these as the eyes are from the vertex. The labium in individuals recently born extends for some distance beyond the caudal extremity of the abdomen, and in nearly all examples of this

instar it extends quite to the tip. It is composed of four segments, with average proportions as follows: First (proximal), 0.129 mm.; second, 0.195 mm.; third, 0.039 mm.; fourth, 0.105 mm. The abdominal segments are distinctly marked by light sutures, and each segment is armed with a series of hairs. Legs prominent; hind legs with the following proportional lengths: Femur, 0.108 mm.; tibia, 0.112 mm.; tarsus, 0.06 mm. Tarsi of two segments; the distal segment bearing, besides the claws, a central spinelike paronychium, two prominent, curved, knob-tipped digitules, and several spinelike hairs; proximal segment small, triangular, and bearing two stout spines. Cornicles circular, elevated but slightly from the surface of the abdomen, surrounded by a series of hairs. Form elliptical in marginal outline, broadest across the middle of the abdomen. Length from vertex to tip of abdomen, 0.64 mm.; width at greatest diameter, 0.24 mm.

Location: Found upon the roots, trunk, twigs, and, occasionally, upon the leaves of the apple and related trees throughout the winter in warm regions (see fig. 2) and during the entire summer in cold ones.

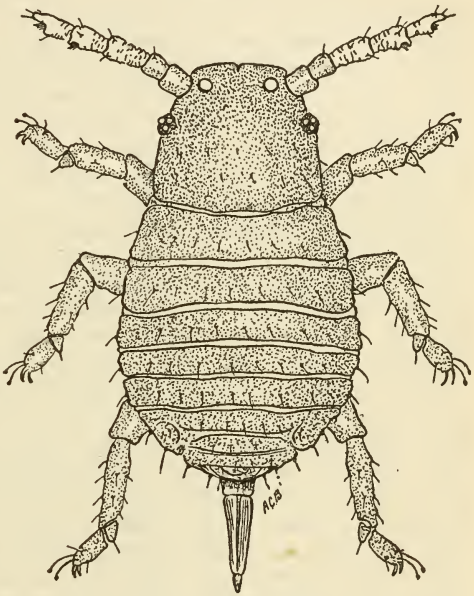

FIG. 2.—*Eriosoma lanigera:* Hibernating wingless viviparous female. Much enlarged. (Original.)

Second instar.—When first molted, reddish brown, with the vertex and appendages shaded, finally becoming dark brown. By transmitted light the color is light brown, with dark-red irregular patches on the abdomen, due to the color within, and with a bright yellow, somewhat transparent, elliptic area extending transversely between the cornicles. This is the wax reservoir (p. 47). Eyes blackish. When freshly molted there is no waxy covering, but this finally develops as a pulverulent bluish-white secretion and a filamentous waxy coat, very sparse upon the head, but prominent on the abdomen, especially in the caudal region.

Morphological characters: Antennæ of five segments, with average lengths as follows: I, 0.03 mm.; II, 0.03 mm.; III, 0.045 mm.; IV, 0.039 mm.; V, 0.048 mm. Sensoria are present on segments IV and V in exactly the same locations as those found in the first instar. They are also of the same nature, but the raised central portions are not so prominent. They do not seem to be so capable of movement as are those of the first instar. More than one sensorium is sometimes found on both of segments IV and V. It is during this instar that the third segment begins to divide. Toward the last of the instar a constriction may be noted where the division will occur, and in the molted skin which indicates the extreme of this instar the construction is quite marked. In some examples, however, the constriction is very slight, and examples of the third instar can be easily found with five-segmented antennæ. The labium is shorter comparatively in this instar than in the first, extending only slightly caudad of the hind coxæ. The cornicles are similar to those of the first instar.

Legs less prominent than in that instar; hind legs with the following proportions: Femur, 0.111 mm.; tibia, 0.114 mm.; tarsus, 0.06 mm. Tarsus as in first instar, with two prominent, curved, knob-tipped digitules. These, however, are not so prominent as in the first instar. The remaining segments of the leg are armed with a number of spines. Form elongate elliptic, with the caudal segments somewhat extended and narrowed. Cauda and anal plate rounded and armed with numerous hairs. Length from vertex to tip of cauda, 0.672 mm.; width at greatest diameter, 0.288 mm.

Location: Same as that of first instar, but this form seems not to hibernate as extensively as does the first instar.

Third instar.—Color when first molted pale brownish, with dusky shadings on vertex and appendages, finally becoming dark brown. Some specimens observed were yellow. By transmitted light the color is light reddish brown, with darker areas and the bright orange-yellow wax reservoir very distinctly visible. As with the other instars, the waxy secretion develops only some time after molting. It is very similar to that in the other instars, but is somewhat more abundant. The secretion from the compound pores may be of the nature of gracefully curving, overhanging waxen threads, or it may be somewhat cottony in nature. This cottony condition is more common in aerial forms, or those kept in moist, dark chambers.

Morphological characters: Antennæ variable, but usually of six segments, sometimes five. Practically all of those examined at the last of the instar have proven to have the antennæ of six segments, while many of those at the first of this stage have five segments. Several have the segment in the act of dividing. The proportions of the segments in both cases are as follows: Five-segmented—I, 0.03 mm.; II, 0.03 mm.; III, 0.054 mm.; IV, 0.036 mm.; V, 0.054 mm.; six-segmented—I, 0.03 mm.; II, 0.03 mm.; III, 0.045 mm.; IV, 0.08 mm.; V, 0.042 mm.; VI, 0.051 mm. Since it is the third segment that divides, the sensoria are found to be situated on the two distal segments. They differ little from those of the other instars either in location or form. The labium extends to the region of the hind coxæ. The legs are still less prominent than in the last instars, the proportions of the hind leg being as follows: Femur, 0.138 mm.; tibia, 0.123 mm.; tarsus, 0.06 mm. The tarsi are similar to those of the earlier instars, with the exception that in most cases the digitules are replaced by simple hairs. The cornicles are similar to those of the earlier instars. Form elongate elliptic, somewhat drawn out caudad. Cauda and anal plate rounded, with numerous hairs. Length from vertex to tip of cauda, 1.22 mm.; width at greatest diameter, 0.56 mm.

Location: Same as in second instar.

Fourth instar.—At first reddish brown, later becoming dark brown or even purplish. Appendages and vertex shaded with dusky. By transmitted light yellowish brown, with wax reservoir showing orange-yellow. Waxy secretion developing after molting, and of two kinds, a pulverulent and a filamentous one. This latter issues as a number of threads from each compound pore, and these threads may fuse into a rodlike structure, or they may remain as distinct threads and become cottony.

Morphological characters: Antennæ composed of six segments, of which the proportions are as follows: I, 0.03 mm.; II, 0.03 mm.; III, 0.039 mm.; IV, 0.03 mm.; V, 0.036 mm.; VI, 0.057 mm. On the distal extremity of VI there are four spines mounted on tubercles and forming two pairs. At the base of the unguis is a group of sensoria, consisting of two or sometimes three. These are circular or oval and fringed, with the center of the largest one raised into a mushroom-like structure. Segment V is armed with a circular fringed sen-

sorium near its distal end, and the center of this is elevated. The labium extends nearly to the hind coxæ. Segments of abdomen armed with a number of spines and the embryo quite visible within, their dark eye spots showing through the integument. The cornicles, as in other forms, are circular, surrounded by hairs, and heavily chitinized on their inner rim. The measurements of the hind leg are as follows: Femur, 0.16 mm.; tibia, 0.176 mm.; tarsus, 0.064 mm. The tarsus is similar to that of the early instars, with the digitules replaced by long simple hairs. The cauda and anal plate are rounded and armed with many prominent spinelike hairs. Form elliptic, abdomen swollen, making insect somewhat pyriform. Length from vertex to tip of cauda, 1.3 mm.; width at greatest diameter, 0.56 mm.

Location: Same as in earlier instars.

Fifth instar (adult).—At first light brown in color, but becoming dark brown or purplish with age. Legs, antennæ, and labium dusky to black. Spiracles, rims of cornicles, and vertex almost black, eyes dark brown to black. The waxy covering begins to show itself soon after molting. The powdery secretion is in evidence over the entire body, and the filamentous secretion more particularly upon the abdomen. In the subterranean forms this is not so abundant as in the aerial, and partakes more of the nature of waxen rods or threads. These are bluish white. In the aerial forms, however, the secretion is often pure white and very fluffy or cottony, forming a large mass which altogether hides the insect.

Morphological characters: Antennæ of six segments, with average proportions as follows: I, 0.06 mm.; II, 0.06 mm.; III, 0.24 mm.; IV, 0.08 mm.; V, 0.09 mm.; VI, 0.08 mm. There is a considerable variation in different individuals from different regions and from different trees. Even the relative lengths do not seem to be constant. The sensoria present are similar to those found in the earlier instars. Besides these there are a number of prominent spines and series of imbrications, particularly on V and VI. These imbrications, as in other instars, are composed of semicircular rows of minute projections. The labium extends to the second pair of coxæ or slightly beyond it. The abdominal segments are armed with rows of small spinelike hairs. Cornicles circular, surrounded by numerous hairs, the ring chitinized more heavily on its inner margin. Measurements of the hind leg as follows: Femur, 0.225 mm.; tibia, 0.204 mm.; tarsus, 0.075 mm. The tarsus has a small spinelike paronychium and is armed with spines and curved spinelike hairs. It has no knobbed digitules like those of the earlier instars. Cauda and anal plate rounded and armed with numerous prominent, curved, spinelike hairs. Outline elliptic, form somewhat pyriform, due to the embryos within the abdomen. Length from vertex to tip of cauda, 1.84 mm.; width at greatest diameter, 1.12 mm.

Location: Same as that given for the earlier instars.

PUPA OF FALL MIGRANT.

(Pl. I, *F.*)

Body brownish, with a reddish or even a purplish tinge; appendages shaded; dark markings not prominent. Covered with powdery wax and with occasionally a few tufts like those of the aptera, only much shorter.

Morphological characters: Antennæ of six segments, with proportional lengths as follows: I, 0.048 mm.; II, 0.064 mm.; III, 0.256 mm.; IV, 0.08 mm.; V, 0.096 mm.; VI, 0.096 mm. The antennæ of the adult alate form are plainly visible within the pupal antennæ, and the annulations may be easily counted. On the pupal antenna itself, however, there are none of these structures, but merely

simple spinelike hairs, with the exception of the sensoria on V and VI. Segment V possesses a distal, circular, fringed sensorium, and there is a group of sensoria at the base of the unguis of VI. This consists of one large fringed sensorium and several small ones. The segment has at its distal extremity several spines situated upon tubercles. The vertex is almost straight and is armed with bristles. The compound eyes, though distinct, do not project prominently; ocular tubercles and ocelli are present. The labium extends to the third pair of coxæ. The wing pads are prominent and 0.8 mm. long; the legs rather slender and with the following relative measurements: Femur, 0.4 mm.; tibia, 0.448 mm.; tarsus, 0.128 mm. Cauda and anal plate rounded and hairy. Length from vertex to tip of cauda, 2 mm.; width at greatest diameter of abdomen, 1.12 mm. Form rather elongate.

Location: Upon the twigs and trunks of apple and related trees among the colonies of apterous forms.

FALL MIGRANT.

(Pl. I, *A*.)

Head black; antennæ and eyes dark brown; thorax almost black, with brown sutures; wings slightly clouded, the veins brown; legs dusky; abdomen brown or purplish. Waxy secretion most prominent on the caudal half of the abdomen, where it forms long downy threads, which often unite into a cottony mass. On the anterior segments of the abdomen the secretion is present as short, irregular, bluish-white tufts.

Morphological characters: Antennæ of six segments, with average lengths as follows: I, 0.064 mm.; II, 0.064.; III, 0.35 mm.; IV, 0.096 mm.; V, 0.102 mm.; VI, 0.08 mm. There is great variation in the antennal segments. Sensoria occur on the four distal segments as follows: Segment III is armed with a series of prominent transverse sensoria or annulations variable in number, but averaging about 18 or 20. These sensoria are upon the underside, but quite a number of them extend more than half-way round the segment, and sometimes several may be seen encircling it. In this respect the fall migrant differs from the spring migrant, for with that form it does not seem common for the sensoria to extend more than half-way round the segment. The upper surface of III has a few scattered hairs on tubercles. Segments IV and V are each armed with four or five of these sensoria, the distal one of V often being a fusion of two. Segment VI is armed at its distal extremity with a number of spines situated on tubercles. At the base of the unguis there is a group of sensoria composed of from one to three oval fringed sensoria similar to those found in the apterous vivipara. Their centers are, however, not so raised as in that form. Besides these there are on the proximal portion of the segment three or four annulations (sometimes wanting) similar to those on the other segments. The most distal of these is usually expanded to form a large star-like area. The labium extends to the middle coxæ. The forewings measure 2.24 by 0.96 mm.; the costa is prominent and slightly curved; the prominent stigma measures 0.4 mm. from the insertion of the subcosta to that of radius. The radial sector is long and not greatly curved. The median vein forks at about its middle and is obsolete for some distance at its base. The cubitus is slightly curved in the direction of the distal extremity of the wing, and the first anal is slightly curved in the opposite direction. The hamuli consist of three fine, overcurving, bristle-like hairs, and the margin of the forewing is thickened to receive them. The proportional measurements of the hind leg are as follows: Femur, 0.448 mm.; tibia, 0.656 mm.; tarsus, 0.12 mm. Between the claws there is a spinous paronychium, and the legs are armed with numerous spines. The cornicles are similar to those of the wing-

less form, the cauda and anal plate rounded and armed with prominent hairs. Form elongate. Length from vertex to tip of cauda, 1.6 mm.; some of the larger specimens are over 2 mm. in length.

Location: In the colonies of wingless forms upon the apple and related trees and upon the trunks of elms depositing the sexes.

MALE.

(Pl. I, *E*.)

Body reddish brown, sometimes with a purplish tinge, usually considerably darker than the viviparous female. Waxy covering delicate, bluish white, downy.

Morphological characters: Vertex rounded. Antennal segments with the following proportional lengths: I, 0.021 mm.; II, 0.027 mm.; III, 0.045 mm.; IV, 0.028 mm.; V, 0.06 mm. Segments II and III armed with a few short spine-like hairs. Segment IV with similar hairs and with a prominent, distal, fringed sensorium, which has a mushroom-like, movable, central projection, and near this usually two or three small, simple, circular, fringed sensoria. Segment V armed on distal extremity with four or five prominent spines. At the base of the unguis is a prominent fringed sensorium, similar to that on IV. Near this are a number of small simple ones, and sometimes an area thickly studded with minute hairs. Labium absent, but the remnants of the trophic tubercle present. Hind leg with the following proportional measurements: Femur, 0.075 mm.; tibia, 0.074 mm.; tarsus, 0.045 mm. Tarsus armed with usually three spine-like hairs and two long knobbed digitules. Between the claws there is a small pad and a delicate spinous process. Abdominal segments armed with hairs, anal and genital plates with many stout curved ones. Claspers small and slightly curved, with a prominent, fan-shaped, chitinized process protruding between them (Pl. XII, *D* and *E*). Length from vertex to cauda, 0.592 mm.; width at greatest diameter, 0.045 mm.

Location: Normally upon the bark of the elm, hidden away in chinks or wandering about in search of females. The writer has taken males at Vienna rarely on the trunks of apple and on small seedlings, and in one instance on the underside of a fallen leaf.

OVIPAROUS FEMALE.

(Pl. I, *G*.)

Color reddish brown, usually quite light as compared with the male, seldom with the purplish-green cast of that sex, unless very old. Waxy covering about the same as that of the male, meager as compared with that of the wingless vivipara.

Morphological characters: Antennal segments with the relative lengths as follows: I, 0.027 mm.; II, 0.027 mm.; III, 0.036 mm.; IV, 0.036 mm.; V, 0.045 mm. In sensoria and other characters the antennæ (Pl. XII, *F*) vary little from those of the male (Pl. XII, *G*). Hind leg with the following measurements: Femur, 0.103 mm.; tibia, 0.105 mm.; tarsus, 0.039 mm. Feet similar to those of the male. Form robust, much broader in proportion than that of the male. No distinct genital armature noticeable. Length from vertex to cauda, 0.8 mm.; width, 0.416 mm. The oviparous female can be easily distinguished from the male by the presence of the large solitary egg showing through the body (Pl. XII, *A*).

Location: Found in the same places as the male, but usually not so active.

SKELETON.

The exoskeleton of the wingless forms is a rather delicate chitinous covering thickened scarcely at all, excepting in such structures as the cornicles, rostrum, and feet. The molted skins are almost transparent. The muscles of the head are supported by a chitinous endoskeleton. This is very much the same in all forms, though the description and figures herein given are those of the stem-mother from elm. In the posterior portion of the head, below the supraœsophageal ganglion, there is a hollow chitinous beam known as the *transverse bar* (Pl. V, *A*, *TB*). This is the main support of the endoskeleton of the head. From each end of it the *antero-dorsal rods* (Pl. V, *A*, *ADR*) pass to the junction of the clypeus and epicranium. From here a chitinous thickening, which we may call the *dorso-lateral rod* (Pl. V, *A*, *DLR*), extends on each side along the lateral walls of the clypeus. The *antero-ventral rods* (Pl. V, *A*, *AntVR*) arise from near the ends of the transverse bar and pass forward laterad and ventrad toward the wall of the head. The *mandibulary rods* (Pl. V, *A*, *MandR*) pass into the head toward the swollen extremity of the mandibles and meet the antero-ventral rods. The mandibles are attached to these rods by their swollen ends. The *maxillary rods* (Pl. V, *A*, *MaxR*) arise a short distance from the mandibulary ones and passing inward fuse with the maxillæ.

In the foot a number of chitinous plates are present which possibly represent segments of the tarsus. The distal segment of the tarsus is surrounded by a broad *chitinous ring* (Pl. V, *B* and *C*, *C*). The *claws* (Pl. V, *B* and *C*, *Cl*) are stout and curved. Between them and the chitinous ring there is a transverse plate of chitin (Pl. V, *B* and *C*, *A*) which when viewed from below has the form of a trapezoid and when viewed from the side is somewhat triangular. In treated specimens this is pierced by two oval openings, as will be seen by the figure. Within the distal segment of the tarsus there is another plate of chitin (Pl. V, *B* and *C*, *B*) which articulates with the transverse plate. This is more elongate than the other and is rounded triangular. A tendon is attached to its proximal extremity. Between the thoracic segments on the ventral portion of the wingless forms there is a chitinous thickening for the attachment of muscles.

In the winged forms the skeleton and endoskeleton of the thorax are quite complex. The *prothorax* (Pl. V, *R*, *P*) is small and bandlike, and when viewed from the cephalic extremity with the head removed is shown to be much smaller in circumference than the mesothorax. The *mesothorax* is very prominent and is divided into distinct parts. The *prescutum* (Pl. V, *L* and *R*, *Ps*) is triangular and small, with its apex pointing caudad. The *scutum* (Pl. V, *L*, *Sc*) is large and bilobed. The *scutellum* (Pl. V, *L*, *Scl*) is peculiar in

shape and may be better understood by examining the figure than by reading a long description. The *postscutellum* (Pl. V, *L*, *PScl*) is directed caudad and ventrad under the metathorax. It is somewhat triangular. The cephalic extremity of the prescutum extends ventrad, forming a small bilobed projection into the thoracic cavity. This is the *anterior phragma* (Pl. V, *L* and *R*, *AP*) and to each of its lobes a muscle is attached. The caudal margin of the postscutellum also extends ventrad to form the prominent *posterior phragma*, which is also bilobed (Pl. V, *J*). The *sternum* is commonly known as the *thoracic plate*, or *sternal plate*. Its shape, when spread out, is shown in Plate V, *D*. When in position it is not as broad for the length as the drawing would indicate. The sternum is divided into four parts, as will be seen by the figure, and it is supported within by surrounding chitinous rods. There is also a *median longitudinal rod* (Pl. V, *D*, *MR*) and a *transverse rod* (*TR*). From that part of the median rod which is caudad of the transverse rod there arises a prominent median *apophysis*. This is somewhat Y-shaped when viewed from the caudal part (Pl. V, *F*), but the stem of the Y is flat, as will be seen in *G*, which is a lateral view. A lateral view of the mesothorax shows it to be thinly chitinized and supported also by a number of chitinized rods. At the anterior extremity three rods arise close together near the sternum and spread as they extend dorsad. Another irregular forked rod is present caudad of these. In a direct line with the chitinous rod of the second coxa a branching rod extends to the base of the forewing. Another rod arises close to this, one branch of which passes cephalad of the posterior wing while the other branch meets its base. Extending inward from the lateral margins of the thorax are small *apodemes* (Pl. V, *H*).

The *metathorax* as seen from above is a small transverse structure, the shape of which is indicated in Plate V, *L*, *MT*.

The *abdomen* is composed of nine distinct segments without considering the *cauda* and the *anal* and *genital plates*, which seem to represent rudimentary segments.

MOLTS.

The different forms of *Eriosoma lanigera* molt four times. Riley, in his account of *americana* (Riley, 1879), states that the sexes of that species have only one molt. In all the sexes of *E. lanigera*, however, that the present writer has reared four molts occurred. Indeed, he has never seen any sexual form of this genus, including apparent *americana* from elms, which did not go through the regular number of molts. In the statement that these sexual forms have only one molt Riley is supported by Miss Patch (1910), who states that the beaks of the females of *rileyi* are lost with "the first (and only) moult." If

this were always the case, it would be a simple matter to separate the sexes of *rileyi* from those of *lanigera*. In the writer's experience, however, the one-molt proposition has never occurred. He does not mean to say that other workers have overlooked molts, but merely states the fact that all his sexual specimens, no matter where taken, molted four times. The duration of the different instars seems to depend considerably upon temperature and moisture. The average length of time between molts of the apterous forms was found to be between five and six days. Under optimum conditions, however—that is, warm (not hot) and moist weather—instars often lasted only three days, whereas under adverse conditions they were found to cover ten or twelve days. For example:

Date of birth.	First molt.	Second molt.
May 4 (conditions good)	May 7 (conditions adverse)	May 15.
May 15 (conditions poor)	May 26 (conditions good)	May 30.

The shortest length of time occupied by any individuals under observation was two days. For example:

Second molt.	Third molt.
May 6.	May 8.
May 21.	May 23.

It is true that some of the sexual forms in confinement did molt in less time than that just cited; for instance, a female born September 20 had the first molt on September 23, the second and third molts on September 24, and the fourth molt on September 30. This, however, seems to have been abnormal. In the following example there are the usual intervals between molts: A female born September 19 underwent the first molt September 21, the second molt September 23, the third molt September 26, and the fourth molt September 30.

DIGESTIVE SYSTEM.

The *alimentary canal* of *Eriosoma lanigera* consists of a rather prominent pharynx extending upward and forward from the buccal cavity; a narrow œsophagus, which passes into a dilated stomach or mid-intestine; a long-coiled hind intestine; and a distensible rectum. The *pharynx* extends through the head above the setæ and bends caudad, forming the œsophagus. It is a narrow tube, slightly dilated in its median portion and armed laterad with rather prominent, chitinized, pharyngeal protuberances. These cause the pharynx, when seen in section, to appear flattened and winged. The swollen portion of the pharynx is armed with muscles, as described under that heading, and the function of these seems to be

to dilate the organ and cause it to act as a pump, taking up the food. Near its entrance into the buccal cavity the pharynx, or a tube representing it, tapers, and its walls are chitinized. In molted skins this portion is plainly visible, and at its upper extremity, in about the situation for the "pharynx protuberances," two curved, eyelike, chitinous structures (Pl. VI, *G* and *G'*) are attached to it. The heavily chitinized walls of this tapering portion of the tube are armed within with prominent folds or teeth, which project into the canal as shown in the figure. It is not improbable that this structure may have the nature of a valve of the epipharynx.

The narrow *œsophagus* extends caudad in the wingless viviparous female until it nearly reaches the first abdominal segment. Here it expands to form the *stomach* or *mid-intestine* (Pl. VII, *E*). In the stem-mother the œsophagus is slightly shorter than in the ordinary wingless viviparous female (Pl. VI, *C*), and in the pupa in the early stages it is much longer (Pl. VI, *D*). At the junction of the osophagus and the mid-intestine the *cardiac valve* is located. In section this appears as a projection of the œsophagus where it is folded back to form the valve (Pl. VI, *K*). The mid-intestine is surrounded by a coat of connective tissue with elongate nuclei, and this bridges the gap between the œsophagus and the wall of the stomach. In section the valve shows a series of cells, each containing a moderately large nucleus. These nuclei extend throughout the valve, although cells are not always visible. A cross-section through the stomach and cardiac valve is shown in Plate VI, *L*. Within the outer coat, which extends also to the œsophagus, the tissue of the stomach is thrown into a series of prominent rugæ or papillæ, in most of which there is a very large nucleus, each nucleus containing a number of dark staining bodies within it. There is a very delicate inner coat lining the stomach.

The *hind intestine* leaves the stomach as a rather narrow tube and is more or less coiled upon itself. Presumably the coils of the adult forms are fairly constant, although in the writer's dissections those of the stem-mother did not seem exactly like those of the summer wingless female (Pl. VI, *C*; Pl. VII, *E*). In the young pupa there was less coiling evident. A glance at the figures showing these coils will save a long description.

The *rectum* extends throughout a good part of the abdomen, and in some specimens observed it was dilated, while in others it was extremely fine and seemed to contain nothing. The rectum opens at the *anus*, which is minute and situated below the cauda. The excrement of the insect is passed out here as honeydew (Pl. VI, *J*). The remarks of Mr. Marlatt (1908) would seem to imply that the species under consideration differs from others in extruding honeydew from the tip of the body. In all the forms, however, that the

writer studied—and these represent numerous genera—the cornicles are not honey tubes but wax-secreting organs, which, although different in structure, are similar in nature to those of *lanigera* herein described.

There are two pairs of *salivary glands*, a small anterior pair and a large posterior pair. These are connected by a duct which passes forward, joins its mate from the opposite side, slightly dilates in the head to form the *salivary duct*, and passes into the salivary pump. Both glands are similar in structure, consisting of an outer coat and a series of large, irregular cells with huge nuceli, each of which possesses a deep-staining nucleolus. In the center of each gland there is an irregular lumen left by the cells which do not quite meet one another, and from this the duct leads out. The anterior gland (Pl. VI, *M*) is one-fourth to one-third as large as the posterior (Pl. VI, *N*). The *salivary pump* (Pl. VI, *E*) is situated a short distance behind the entrance of the pharynx into the buccal cavity. The structure to which the writer refers seems to agree with the description of that organ given by Davidson (1913), though he is certainly unable to make out any such elaborate structure as that described by Krassilstschik (1893) for Phylloxera. It can not be that Davidson, at least, was referring to the pharyngeal pump, which the writer has previously described, as the latter also finds that organ mentioned by him, which is in a different position from the one under consideration. In fact, the structure (Pl. VI, *F*) seems to be a simple goblet-shaped piece of chitin covered with a membrane. The membrane is folded down into the goblet, and the large pump muscles are attached near its rim. As in other aphides, the malpighian tubules are absent entirely.

The *mandibular retorts* are elongate, somewhat retort-shaped organs, attached to the enlarged extremity of the mandibular setæ. They are composed of a mass of small cells and a few scattered larger ones enclosed within a layer of epithelium, the whole being surrounded by a membrane. The *maxillary retorts* are similar structures attached to the large extremity of the maxillary setæ. In the adult these retorts are not so large and distinct as in the earlier stages, particularly in the embryo, where they may be seen with the setæ coiled about them. The setæ appear to be produced from the pointed extremity of the retorts, but no theory is here advanced in regard to the nature and function of these structures. It may be mentioned, however, that in sections through retorts and lobes of the brain both stain considerably alike, and at the base of the retort, where it joins the seta, fibers may be seen extending into the funnel.

The food is taken up by means of the *setæ*, three fine threadlike organs which play along a groove in the labium. There are in reality

two pairs, one pair of which has fused. Those representing the mandibles (Pl. VI, *I*, *Mnd*) are located below the pharynx and are attached to the mandibular rods. (See Skeleton.) They are swollen funnel-shaped near their proximal extremity, but become minute setæ on entering the groove in the labium. A fine canal extends throughout each to its extremity. Those representing the maxillæ arise close to the mandibular setæ and are similar in shape at their origin. These two, however, fuse before entering the labial groove and form one continuous tube between the mandibles. A cross section of the labium (Pl. VI, *I*) shows that on the floor of the groove in which the setæ play there is a heavy layer of chitin. In regard to the setæ themselves, the writer does not find them similar to those of the cicada, in that there is no such sclerite attached to their proximal extremity. There is nothing similar to that figured by Sanborn for *Longistigma caryæ* Harris, unless, indede, it be the mandibular rod.

In the sexual forms the digestive system is rudimentary, and during the entire life of these insects they take no nourishment. The alimentary canal is in some cases represented, but it is shriveled and seems to have no definite shape. Where seen it is usually as represented in Plate VI, *B*, shrunken and degenerate. In one instance, however, in examining a male of the first instar the region of the cardiac valve was seen to be present in recognizable form. The narrow œsophagus was present as in other forms, and something of a distinct enlarged stomach, or mid-intestine (Pl. VI, *A*).

In his description of *americana* Riley (1879) states that the sexes are born with a stout promiscus which is lost on molting. This, however, is not the case with *lanigera*. Bearing this point in mind, the writer looked over hundreds of sexes of *lanigera* in all ages, and in not one instance was a labium similar to that of the other forms present. He has also watched the forms at birth and examined them immediately upon the rupturing of the sac, with the same results. The nearest approach to a beak that was observed is a somewhat rudimentary *trophic tubercle* (Pl. VI, *H*). Sexual forms of *americana* observed sometimes had quite a distinct labium.

INJURIES.

The puncturing setæ and the fluids inserted during feeding are supposedly the cause of the tumors and gall formations produced by this species. That there should be such a variety to these formations is, however, somewhat surprising. *E. lanigera* affects leaves, stems, roots, and fruit.

Upon the elm the stem-mother and those forms succeeding her affect the leaves so as to force them to curl or twist, forming a

rosette (Pl. VIII, *C*) or sometimes a definite curl. This last, however, is more commonly produced by *americana* (Pl. VIII, *A*). This curling or twisting of the leaves seems to be due to the unequal growth of the leaf surface, that upon which the insect is feeding being retarded. The curled part of the leaf often changes color, becoming yellow or even red. While this twisting of the leaves is very common upon the elms, the writer has searched for a long time in vain for an example upon the apple in nature. By infesting a seedling apple with the species he was, however, able to get a twisted leaf (Pl. VIII, *B*) that fairly well approaches the form of those leaves in rosette on elm. This action of the species must, however, be rare. In another instance he took from an apple tree a leaf curled much as elm leaves are curled by *americana*, and within the curl was a thriving colony of *lanigera*. They may not, however, have been the original cause of the curl.

The most common, as well as the most serious, result of the feeding of this "louse" is met with upon the twigs (Pl. IX, *B*) and roots (Pl. IX, *A*) of apples. On young seedlings this is so bad as to deform them and make them unfit for sale, and at Vienna, Va., two and three year old trees were killed outright during the course of the writer's experiments. The constant feeding of the aphides upon the roots and twigs alters the tissue considerably, which fact is easily demonstrated by means of a few sections. In a young gall there is slight alteration in the periderm, or cortex, that which is present being easily due to the pressure from within, with the exception, perhaps, of a slight decrease in sclerenchyma. Over the gall it is impossible to separate the bast from the cambium, while this is easily accomplished elsewhere. A large portion of the wood usually also forms part of the gall. The cells here are thin and contain elongate nuclei and, notably, a large quantity of sugar. There is little starch compared to that in the normal tissue.

This fact of the presence of large quantities of sugar led the writer to conduct a series of experiments. Supposing that possibly some amylolytic ferment might be responsible for this presence of sugar, he carried on a series of injections into the cambium, first of human saliva and secondly of a solution made by mashing that portion of the insect containing the salivary glands in water. (It was found impracticable to dissect out a sufficient quantity of these organs.) The experiments were begun in the spring at the time when the aphides were beginning to work, so as to take advantage of the growth of the twigs. No favorable results, however, were shown in either case and the idea of artificial gall formation was abandoned. No attempts were made to produce galls upon the roots.

The wingless form of this species is sometimes found deforming apples upon the tree. They appear to enter at the calyx end and

are met with even within the core. In one instance, however, the writer observed, at Vienna, Va., a York Imperial with the stem of the apple deformed and wingless individuals crowded far down in a cavity about it. The writer is unable to note any published account of this core infestation.[1] It seems to be uncommon but widespread. The following note by Prof. Quaintance shows its occurrence in the West and the writer has observed it in Canada.

Wash., D. C., Nov. 30, '08. In cutting open some western apples, find the core infested with a considerable colony of wingless insects of this species (*lanigera*) of various sizes from breeding lice to newly born. The calyx cavity extends in a small channel to the interior through which the insects first made entrance, no doubt, and through which they escape. A. L. Q.

Eriosoma lanigera has also been accused of transmitting diseases of the apple, Descours-Desacres (1901) concluding—

Le purceron lanigère, qui est un agent actif de transmission du chancre sur le pommier, semble donc ne pas préparer seulement sa voie au *Nectria ditissima*, mais bien *ensemencer lui-même*, par l' *apport de mycelium* ou de spores de Nectria, les plaies faites par lui ou la plaie accidentelle sur laquelle il s'est établi.

BODY FLUIDS.

The dark brown or wine color so often met with in this species is due to the color of the body fluids. These are of such a nature that when the insects are crushed they appear as if filled with blood. Such appearance has given rise to one of their common names, i. e., "Blutläuse," so extensively used in German writings. A similarly colored fluid occurs in *Lachnus viminalis* Boyer, a form feeding upon the willow. It has been studied by C. J. Muller (1881) who concludes that the colored substance is similar to salicin, belongs to the juices of the tree, and is not a definite product of the insect. It seems strange, however, that so many species feeding on such a variety of plants should have a character so similar if this is the case. Moreover, there often occur upon the same tree different species of aphides some of which are blood colored and others yellow or green. The writer has been unable properly to study this subject with respect to *lanigera*, and such experiments and observations as he has made are very primitive and scarcely worthy of record. It may be noted, however, that most of the species showing this blood color to a marked degree are bark-feeders.

MUSCLES.

The muscles in all forms of the species have been studied by the writer. Those of the stem-mother and spring migrant are here de-

[1] Since the foregoing was written there has appeared in England an article by Hewitt (1913) in which this same occurrence is noted within the core.

scribed. Both of these forms were believed by students of the Aphididæ to represent another species, *americana*. The comparison of the structure of these two forms with Davidson's observations and with the writer's anatomical studies of summer and fall *lanigera* proved that *americana* was a compound species claiming three generations of *lanigera*. The writer was thus able, by aid of these anatomical details, to connect forms of very different habits and so build up the complete life history.

MUSCLES OF THE HEAD.

Anterior divaricator muscles of the pharynx.—These are attached to the antero-dorsal wall of the pharynx and extend to the anterior wall of the clypeus. They are band-shaped and rather narrow where attached to the pharynx, but broaden as they reach the clypeus. One of these, the uppermost, is opposite in form, being fan-shaped, with its broadest extremity attached to the pharynx. The opposite end of this is attached at the junction of the clypeus and epicranium. (Pl. XI, *A*, *ADMP*.)

Lateral pharyngeal muscles.—These are attached to the pharynx in the region of the protuberances and passing outward become attached to the lateral walls of the clypeus. These muscles, together with those mentioned above, control the pumping action of the pharynx. (Pl. XI, *A*, *LMP*.)

Muscle of the salivary pump.—This is a large, spindle-shaped, divided muscle, attached to the transverse bar and extending to the salivary pump, near the rim of which it is inserted and the movements of which it controls. (Pl. XI, *A*, *PM*.)

Elevators of transverse bar.—Each of these is a band-shaped muscle extending from the transverse bar antero-dorsad of the epicranium. They are slightly fan-shaped. (Pl. XI, *A*, *ElTB*.)

Depressors of transverse bar.—The depressors extend on each side from the transverse bar to the caudo-dorsal border of the head, and are there attached very close to the cephalic end of the median longitudinal dorsal muscle. (Pl. XI, *A*, *DpTB*.)

Ventral pump muscles.—These are two small muscles extending from the salivary pump to the ventral chitinous rods.

Retractors of the maxillæ.—One of these muscles is attached to the enlarged proximal extremity of each maxillary seta and extending below the retractor muscle of the mandible is attached to the antero-ventral rod of chitin. (Pl. XI, *B*, *RMx*.)

Retractors of the mandibles.—These muscles are attached one to each of the mandibular setæ on the inner part of its enlarged proximal extremity and extend to the antero-dorsal rods. (Pl. XI, *B*, *RMd*.)

Protractors of the maxillæ.—These are attached one to each maxilla on the ventral portion of the swollen proximal extremity. They extend to the antero-ventral walls of the "frons." (Pl. XI, *B*, *PMx.*)

Protractors of the mandibles.—These are rather powerful muscles and are attached to the mandibular rods, from which they pass to the antero-lateral walls of the frons. Since the mandibular rods are attached to the mandibles, any action upon them is conveyed directly to the mandibles. (Pl. XI, *B*, *PMd.*)

Elevators of the antennæ.—These extend from the anterior dorsal rod on each side of the anterior dorsal insertion of the antennæ. (Pl. X, *C*, El_{1-3}.)

Depressors of the antennæ.—The depressors also are attached to the anterior dorsal rods and extend to the more ventral caudal portion of the first antennal segment. There are other depressor muscles which have a different position. These pass from the base of the second segment, near the attachment of the above, to the wall of the first segment on the opposite side. (Pl. X, *C*, Dp_{1-3}.)

Elevators of second antennal segment.—These are attached to the base of the second segment and extending downward are fastened to the base of the first segment. (Pl. X, *C*, El_2.)

Depressors of third antennal segment.—These are attached to the base of the third segment and extend backward to the base of the second segment. (Pl. X, *C*, Dp_3.)

Elevators of the third antennal segment.—These muscles are very similar in shape and position to the depressors, excepting that they are placed on the opposite side of the segment. (Pl. X, *C*, El_3.)

Muscles of the rostrum.—What seem to be the elevator and depressor muscles of the rostrum are attached to the proximal border of the second labial segment and passing through the first segment and around the thoracic ganglion are fastened to the dorsum of the prothorax. (Pl. XI, *E.*)

MUSCLES OF THE THORAX.

The system of thoracic muscles in the stem-mother and wingless viviparous female is simple and corresponds to a great extent to that of the abdomen. They may be considered as follows:

Longitudinal ventral muscle.—This is a narrow band situated near the median line on each side and extending from the cephalic margin of the prothorax to the cephalic margin of the first abdominal segment where it meets the median longitudinal muscle of that segment. It is divided usually into two fasciculæ and is narrower on the prothorax than more caudad. (Pl. X, *A.*)

Median longitudinal dorsal muscle.—This muscle is a narrow band on the prothorax either side of the median line and extending

from the cephalic margin of that segment, near where the depressor of the transverse bar is attached to the head margin, to the caudal margin of the segment. In the remaining portion of the thorax it is considerably broader, being there equal to both dorsal muscles of the thorax.

Lateral longitudinal dorsal muscle.—This muscle is found only in the prothorax, extending from its caudal margin, where it is close to and almost a part of the median muscles, to the latero-dorsal cephalic margin. (Pl. X, *A*.)

Dorso-ventral muscles.—These are small strands usually situated three together and connect the dorsum and venter. In the prothorax there is one bundle on each side attached to the venter near the longitudinal ventral muscle and near the caudal margin. On the caudal margin of the thorax there is one bundle arising near the longitudinal muscle and one bundle more laterad, near the cephalic end of the lateral ventral muscle of the first abdominal segment. (Pl. X, *A*, *DVM*.)

In the winged forms the muscles of the thorax are much modified for purposes of flight, and for the attachment of these muscles the thorax itself is necessarily very different from that of the wingless form. In the prothorax the muscles are much the same as in the wingless form, though apparently not so broad. In the mesothorax, however, they are very different indeed. They may be considered as follows:

Lateral longitudinal dorsal muscles.—These muscles, one on each side, extend from the rounded dorsal portions of the scutum or "thoracic lobes" to the lateral portions of the posterior phragma. They are narrow and somewhat cylindric. (Pl. XI, *J*.) The position of each of these muscles on the phragma is considerably dorsad of the median longitudinal muscle on each side, as will be seen by Plate XI, *H*.

Median longitudinal dorsal muscles.—Attached, one to each of the lobes of the small triangular anterior phragma, are the median muscles. They are narrow, somewhat cylindric, and extend caudad, passing below the caudal portions of the lateral muscles, and are attached to the posterior phragma. They are situated close together. (Pl. XI, *I*.)

Great dorso-ventral muscles.—These consist of two very large muscles on each side extending from the "thoracic lobes" above to the sternal plate beneath. (Pl. XI, *K* and *G*.)

Smaller dorso-ventral muscles.—These muscles, best observed in the pupæ (Pl. X, *F*), are somewhat spindle-shaped, being narrow where attached to the dorsum just above the wing pads, but somewhat broader where attached to the sternal plate.

Longitudinal ventral muscles.—These muscles are attached to the anterior rounded portion of the central apophysis. They are very

small, narrow, threadlike muscles. The lateral one on each side extends to the caudal margin of the prothorax, while the median ones extend farther cephalad. (Pl. XI, *K*.)

Lateral muscles.—Extending from the lower surface of the arm of the central apophysis on each side to the latero-ventral walls of the thorax is a band-shaped muscle (Pl. XI, *G*), and from the upper and outer extremity of the arms, narrow cylindric muscles extend to the region of the legs. (Pl. XI, *D*.)

Longitudinal muscles of metathorax.—On the dorsum there is a small band on each side close to the median line, just caudad of the large median longitudinal muscle of the mesothorax. On the ventral surface a similar band is present. (Pl. XI, *K*.)

Flexors of the legs.—From the posterior margins of the thoracic segments muscles extend to the posterior surfaces of the coxæ, two to each.

Flexors of tibia.—Since the trochanter is anchylosed to the femur, these two segments act as one so far as the muscles are concerned. Attached to the inner face of the trochanter and extending throughout the femur, to be attached to the inner edge of the tibiæ, there is a rather stout flexor muscle. It narrows considerably near its attachment to the tibiæ. (Pl. X, *E*, *FlxTib*.) Attached to the tibiæ in nearly the same position are a number of muscles which extend diagonally across the femur and are attached along its outer face. These are tendonous at their insertion on the tibiæ, but broaden as they reach their attachment on the femur. (Pl. X, *E*.)

Extensor of tibiæ.—At the junction of the trochanter and femur, on the outer surface, there is a somewhat tendonous insertion of a spindle-shaped muscle. This extends throughout the femur and is attached to the rounded portion of the tibia which projects into the femur. This in reality seems double, formed of two similar muscles. (Pl. X, *E*, *ExTib*.)

Flexor of tarsus.—At the distal extremity of the tarsus there is a muscle which spreads into several fan-shaped parts; each of these at its larger extremity is attached to the walls of the tibiæ and at its narrow extremity is fastened to the inner edge of the proximal segment of the tarsus. (Pl. X, *E*, *FlxTar*.)

Extensor of tarsus.—At the proximal extremity of the tibia, on its rounded outer portion, there is the attachment of a rather broad muscle. This narrows as it extends distad throughout the segment and is attached to a tendon which extends proximad through the tarsus from the chitinized plates of the foot. (Pl. X, *E*, *ExTar*.)

MUSCLES OF THE ABDOMEN.

The muscles of the abdomen, both in the wingless and the winged forms, consist of two systems, a longitudinal system and a dorso-

ventral system. These are both segmental, the longitudinal muscles extending from the cephalic margin of a segment to its caudal margin where it meets the cephalic extremity of the segment more caudad. The dorso-ventral muscles extend from the venter of the segments to their dorsum. (Pl. X, *A;* Pl. XI, *K.*)

Median longitudinal ventral muscles.—These consist of a series of muscles, one for each segment covered, forming a band extending near the median line from the cephalic portion of the first abdominal segment to the eighth. The muscle in each segment is composed of a number of fasciculi. In the wingless forms three of these are frequently met with in each muscle, while in the pupæ two seem invariably the rule. (Three are shown in the figures of the wingless female.) In the wingless forms the median longitudinal muscles of the thorax appear as a continuation of this band of muscles. (Pl. X, *A.*)

Lateral longitudinal ventral muscles.—These muscles are very similar to those of the median band. They are located about half way between the margin and the median band, and cover the same segments. These two are usually composed of three fasciculi in the wingless forms and two in the pupa. Often, however, narrow ones in the aptera have only two.

Dorso-ventral muscles.—There are, in each segment possessing a longitudinal muscle, usually three dorso-ventral muscles on each side. These are attached close to the caudal margin of the segment and just laterad of the longitudinal muscle. They arise close together. In the pupæ they are farther away from the longitudinal muscle than in the aptera.

Median longitudinal dorsal muscles.—Corresponding also to the lateral ventral band is a lateral dorsal band for the same segments. It is very similar to the ventral band in location and number of fasciculi.

Muscles of the cornicles.—The opening of each cornicle is controlled by a special muscle which extends from the inner liplike structure down through the body to the eighth segment. When this muscle contracts, the lip of the cornicle is drawn back upon itself thus opening the cornicle, as explained under "Cornicles" (p. 47). Pl. XIII, *F* to *I.*)

Muscles of spiracles.—Besides the dorso-ventral muscles proper, some bands are attached near the spiracles and pass inward therefrom. These, together with the true dorso-ventral muscles, serve to effect respiration.

Muscles of genital opening.—The muscles moving the genital opening of the female during the act of parturition might be included with the abdominal muscles. They seem to be a kind of extension

of the abdominal system, but are slightly different in arrangement, as will be seen from figure 3. There is a band of muscles (*D*) on each side, extending around the most distal extremity of the body. From the union of the two distal segments on each side there are two bands of muscles, one (*C*) extending transversely across, caudad of the opening, the other (*B*) extending somewhat cephalad to the margin of the opening. From the lateral margin of the segment cephalad of that on which the other muscles are attached there is a band (*A*) on each side extending caudad and mesad toward the orifice. The vagina itself also has a series of muscles.

MOVEMENT.

As discussed under reproduction, the young of *Eriosoma lanigera* are born within a closed sac. They are retained, however, by the mother until they are capable of moving about. As soon as deposited the young aphis moves its antennæ and feet restlessly and soon starts off in search of food, testing many places with its beak. In this early stage the young move about quite freely, and it is at this time that migrations of the wingless forms occur. After becoming more mature and settling down the aptera seldom change their location, and indeed they nearly always die on being transferred. Both spring and fall migrants are capable of comparatively long flights, although they are by no means strong-flying insects.

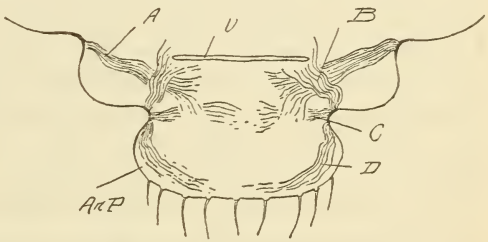

FIG. 3.—*Eriosoma lanigera:* Muscles of caudal extremity (*A, B, C, D*), showing also vulva (*F*) anal plate (*AnP*). Greatly enlarged. (Original.)

MIGRATIONS.

Migrations are made by the wingless forms as well as by the winged ones. The first migration might be said to take place with the stem-mother. Upon hatching from the egg the young of this form wanders up the trunk or along the limb of the elm upon which she finds herself until the base of a bud is reached. Here she settles, waiting patiently for it to open. The writer has observed these forms at Vienna, Va., for a week or ten days before the opening of the buds. As soon as the buds open, the attack of the insect causes the leaves to twist or "rosette" about her.

The second migration in point of time is effected by the spring migrants. This extends over a long period, beginning at Vienna, Va., early in May and extending well on into June. The spring

migrants prefer fine days for migration. During the beautiful warm spring days one crawls from the rosette until she has reached a leaf rather more prominent than the others, and from this she flies upward for a considerable distance, then drifts slowly along in the air until, if fortune favors her, an apple tree or another of her summer hosts is reached. It is easy to trace this migration in nature by attaching small bits of white silk thread to the insects, whereby they may be known again. In this way the writer succeeded in capturing on apple trees known specimens from elms. In the greenhouse he also transferred many hundreds of insects collected from elms to apple seedlings, where they reproduced until he again returned the fall migrants to the elms.

Upon reaching the apple trees the spring migrant usually selects the under surface of the leaves and the tip of the twigs or water sprouts. Here she deposits her young along the mid-vein or upon the petioles or twigs. This generation is wingless, and in the writer's experience it migrates little. The following one, however, does so in considerable numbers, wandering along the limbs and down the trunk to attack the roots. On all the seedlings supplied with this fifth generation the roots were badly attacked from the "lice" wandering down from above. This seems, from the viewpoint of control, rather interesting. At Vienna, Va., this generation from known parents was present from July 1 until the beginning of August.

The sixth generation constitutes most of the fall migrants, and these have a return migration to the elms from apple and related trees. This migration begins at Vienna, Va., about the middle of September and continues even to November. The fall migrants are the commonly known winged forms of the woolly aphis. They migrate during the beautiful weather of fall and Indian summer. Crawling to the tips of the twigs, they float away through the fading afternoon sunlight, and in the evening they may be found in the crevices of the bark of the elms, there depositing the sexual forms. In the winter their dead and shrunken bodies may be still seen clinging to the bark and are a good indication of the proximity of eggs.

The sexes take up their life upon the elm bark, mate, and the female lays its egg.

There is yet one other migration, which is produced by wingless forms in the early spring. These are generally first-instar aptera (fig. 2) which have existed upon the roots or in sheltered places during the winter. They are more green in color, as opposed to the brownish color of the nonhibernating ones. The winter, in so far as the writer's experience goes, kills all but these very young forms—at least, all above ground. Many of those upon the roots migrate upward in spring.

REPRODUCTION.

REPRODUCTIVE SYSTEM.

Eriosoma lanigera, like other members of the family Aphididæ, reproduces for a greater part of the year by parthenogenesis. This is the method of all forms, except those of the last generation in the autumn, i. e., male and oviparous female.

The reproductive system in the viviparous form is most easily studied in the wingless female. In examining such a form the *vulva* will be noted as a slitlike opening between the anal plate and the genital plate and extending across the caudal extremity of the abdomen. Leading inward for the distance of about two segments is the *vagina*, a muscular flattened tube which appears broad when viewed from above, but narrow when viewed from the side. (Pl. VII, *D.*) Opening into the vagina are two *oviducts*, one on each side of the body, and from each oviduct four *ovarian* tubes lead cephalad. In the mature insects the developed embryos in the chambers of these tubes distend the abdomen considerably. It is, in fact, very difficult to make out the reproductive system in mature forms, the younger ones showing it to much better advantage. It is only from the embryo that a perfect knowledge of this system can be derived. In the ovary of the early embryo differentiation of the cells can be noted. The egg cells can be distinguished from the nutritive cells in that they are situated in the lower part of the chamber, are smaller, and do not possess the large, heavily staining nucleolus of the latter. When the first egg cell passes out of the chamber the epithelium of the tube contracts behind it, and so forms the first egg chamber. The egg, however, remains connected for some time by a threadlike portion. Finally, when the embryo is fairly well developed, it is followed down by another egg cell, until the ovarian tube with its numerous chambers is formed.

The oviparous female is remarkable in that she lays only one egg, while the wingless viviparous forms produce a large number of young. Long before the female is born her egg is fairly well developed. In order, therefore, to make out the reproductive system in this form we must go to the embryo as it is found within the ovarian tubes of the fall migrant. Young embryos here show that the ovaries are at first similar to those of the parthenogenetic form. There may be distinguished the four chambers on each side containing egg cells and nutritive cells. In later embryos most of the egg tubes are in the process of degeneration and only two ovaries, one on each side, develop. Of these one finally degenerates and the egg of the other grows until it fills almost the entire body and the insect appears to be little else than egg. (Pl. XII, *I.*) There are two small accessory

glands present in this form, one on either side of the vagina, and similar ones may therefore be present in the viviparous female, though I have not noted them.

The external genital organs of the male (Pl. XII, *D*) consist of a pair of short, slightly curved *claspers* situated one on each side on the ventral caudal extremity. From between these there protrudes a *large fan-shaped structure* which when viewed from the side (Pl. XII, *D*), is slightly curved upward and when viewed from below has much the shape of the tail of a brook trout. This organ is chitinized—more so upon the sides than in the middle, where it is membranous. It has its broadest end caudad (Pl. XII, *E*). Between this organ and the small claspers there is sometimes seen protruding the large, fleshy, somewhat pointed, recurved *penis* (Pl. XII, *D*, *P*). This, however, is not very often seen in mounted specimens, and none of the structures just described is visible in the early instars. Even when the chitinized structures are present, the penis is usually retracted. The *testes* (Pl. XII, *K*, *Ts*) are situated close together, so much so that they often appear as one structure. Each is somewhat globose, but drawn out at the extremities. Within each testis may be seen a number of parts which are shaped like the ovaries on the head of a buttercup. Each one of these is composed of a large number of threads lying side by side and appearing not unlike the figure given by Berlese (1909) for *Mytilaspis citricola* Comst. Leaving the testis the *vasa deferentia* (Pl. XII, *K*, *Vd*) appear as narrow tubes coiled upon themselves. These finally dilate into the *seminal vesicles* (Pl. XII, *K*, *SV*) and enter close together into the *ejaculatory duct* (Pl. XII, *K*, *EjDct*), a globular structure at the caudal extremity of the abdomen. Near the entrance of these is also noticed the entrance of two large but somewhat narrow and elongate glands, one on each side (Pl. XII, *K*, *Gd*).

PARTURITION.

As the embryos develop they pass down the oviducts through the vagina and are expelled from the orifice while still enclosed within the membrane. Breach presentation is the normal method. By a series of contractions of the body the young is forced out until about two-thirds of its body is exposed. At this juncture the membrane sometimes ruptures, while in other cases it does not do so until the mother has lost her grip on all but the head of the young. She retains her grip upon the head for a considerable period, and during this time the young insect frees its legs and moves them about constantly, apparently getting them in readiness for use. When finally the mother releases the young altogether the remnant of the membrane generally comes away during this act, though in some cases the young removes it with its forelegs. The entire length of time

taken for the operation, as observed on forms in captivity, is about 30 minutes, and about half of this time is occupied before the legs are freed. Wax appears upon the young almost immediately.

With the winged forms, giving birth to young seems to be a much simpler performance. In fact they seem almost to drop their young. Migrants from elm when placed upon apple leaves deposited their entire quota of young in a very few minutes, dropping them one after another at an astonishing rate. With these forms the young do not begin to move until some time after they have been deposited. They are often born entirely in the membrane and free themselves upon the leaf. With the wingless forms, however, when the young are born in this condition they have little chance of living, so far as the writer's observations go.

After the wingless form has produced her young she may be distinguished from one that has not done so by the somewhat shrunken condition of the abdomen. This, however, is no more than would be expected under the circumstances. With the winged forms, on the contrary, the shrinking of the abdomen is so great that when these insects have reproduced they appear to have scarcely any abdomen at all, and what is present is shriveled up against the thorax. In the ovipara this condition is still more marked (Pl. XII, *H*), owing perhaps to the smallness of the thorax.

The process of egg-laying by the female consists more in contracting away from the egg than in extruding it, for the egg when laid is much larger than the shriveled remnant of the insect which laid it. Although believed by some to be the case, the mother does not die immediately upon producing this egg. The writer has seen females which have deposited remain alive for some time and has watched these peculiar shrunken remnants walking about.

NUMBER OF YOUNG.

The number of young deposited by the wingless forms during their lifetime seems to vary considerably, depending on food supply and weather conditions. The stem-mothers, however, deposit by far the largest number of young. One of these kept in confinement during late May and early June produced in all 299 young. Others were seen to produce as many as 20 young in a day. As a rule, however, when a large number of young were produced in one day few would be born during the succeeding few days and often none for two or three days. With the summer wingless forms the number of young produced in confinement was much less than with the stem-mothers, 30 being usually about the number and an average of only 3 a day being born. All those, however, of which counts were kept were fed on roots and kept in underground conditions

similar to those surrounding the major part of the insects at that time of the year. The number of young produced by the winged forms is much smaller, being 6 on an average. The oviparous female never lays more than one egg.

COURTSHIP.

Courtship between sexes of this species often lasts several hours and sometimes occupies as long as two days. The females are usually inactive unless approached by the males. These latter, however, are far from inactive, especially after the last molt. Copulation never appears to take place unless both sexes are mature, and one male usually serves more than one female.

WAX SECRETION.

Like related species, *Eriosoma lanigera* is covered with a secretion of wax. This varies considerably as between the different forms, being most abundant in the aptera. The waxy covering consists first of a bluish-white, powdery substance, which is scattered over the body, giving the insect a mealy appearance. This is present on all of the forms, but is not seen immediately after molting. Secondly, there is a filamentous secretion from the compound wax pores. This is, in the subterranean and some aerial forms, bluish white and composed of distinct, rather long, waxen threads, which arise from the pores and curl downward in beautiful ribbons. Again, particularly in the aerial forms, it may become fluffy and perfectly white like cotton. It is from this secretion that the insect derives its popular name, "woolly aphis." This waxy secretion is most abundant on the caudal portion of the insect, where it forms long streamers. On the anterior portion of the body these tufts of wax are short. The winged forms have very little of this prominent secretion. In the sexes it is present, but in a limited supply, and is very delicate in nature. The egg after being laid is covered with a quantity of this white waxen material. This wax is extruded very quickly, for when insects were perfectly denuded they would, a few hours later, be covered again as completely as before denudation.

Scattered over the body are a number of *compound wax pores*, the nature of which the writer has studied in the wingless viviparous female. In this form these pores are located as indicated in Plate XIII, *A*. Each of these pores consists of a ring of large cells, averaging about eight in the largest pores. (Pl. XIII, *C*.) There are, however, a number of smaller pores, as those on the head and caudal portion of the abdomen. These are composed of three or four cells and usually do not form a ring, but are placed compactly together. In the winged forms the cells are more numerous. (Pl. XIII, *C′*.)

In section each cell shows a rather deep structure below the integument in the center of which is a cavity termed the *wax chamber.* (Pl. XIII, *D.*) The marginal portion of this arrangement consists of a wax-secreting body which pours the wax into the chamber. From here it passes out to the surface and takes the form as described. There is a large nucleus usually situated below the wax chamber.

Besides the wax from the compound pores, a wax is also passed out at the cornicles. This, however, is not white or bluish white as that previously mentioned, but is yellowish. The *cornicles* are two structures placed on the dorsum between the fifth and sixth abdominal segments. They consist of a ringlike opening rather heavily chitinized on one-half its margin and an outer part surrounding the ring which is somewhat striated and armed with a number of spines. The whole structure (Pl. XIII, *E*) is slightly elevated from the surface of the abdomen. The opening and closing of the cornicle is most easily explained by reference to Plate XIII, *F* to *I*. It will be seen that a muscle is attached to the liplike fold which closes the cornicle on the side opposite to the heavily chitinized one. By contracting, this draws the lip backward upon itself (Pl. XIII, *G* and *I*), leaving the cornicle open. Extending from each cornicle is a small duct which leads to a large football-shaped sac lying transversely across the caudal portion of the abdomen. This *duct* (*Dct.*, *H* and *I*, Pl. XIII) is for the passage of the wax into the cornicle. We may call the sac the *wax reservoir*, as it is always filled with wax and can be seen as a yellowish, partially transparent body within the abdomen. In alcohol it becomes white and opaque.

The wax-secreting structures in this group of Aphididæ are worthy of careful study, for they are sometimes one of the simplest means of distinguishing closely allied species.

RESPIRATION.

The respiratory system consists of a dorsal and ventral system of *tracheæ* supplied by a row of nine spiracles on each side. The first two pairs of spiracles are situated upon the prothorax and metathorax, the mesothorax being devoid of them. The remaining seven pairs are placed on the first seven abdominal segments on the venter near the margin.

The *spiracles* are chitinized, ringlike openings situated upon the abdomen and thorax, as previously mentioned. When looked at from straight above the opening each appears like a ring more heavily chitinized on one side (Pl. VII, *C*), from which there extends a cylindrical tube. In looking at a spiracle, partly from the side and partly downward, it becomes evident that the chitinized portion seen previously is triangular, extending from the orifice some dis-

tance cephalad. (Pl. IV, *M*.) The part of this tube which is outside of the body is triangular and more heavily chitinized than that within the body. From the inner wall of the outer chitinized triangular part of this tube a chitinized piece (Pl. IV, *M*, *b*) extends downward into the tube. This very nearly meets a curved chitinized piece (Pl. IV, *M*, *a*) extending upward from within the body. The space between these two is narrow and in that region the trachea (Pl. IV, *M*, *Tr*) is very fine. It soon dilates, however, and usually extends caudad as indicated in the figure.

Extending inward for a short distance from each spiracle is an unbranched trachea. From this in turn there are given off two smaller tracheæ, one of which is extended to join the dorsal longitudinal trunk and the other the ventral. This is best seen in the wingless viviparous female (Pl. VII, *A* and *B*). In this form the *dorsal tracheal system* consists of two longitudinal lateral trunks and one caudal arch uniting them. In the abdomen these trunks are regularly and acutely zigzag, but in the thorax the trunks are almost straight. From the basal trachea from each spiracle a branch extends mesad to join one of the angles of the lateral trunk on its side, and each of these branches is again branched cephalad at about midway between its origin and its union with the longitudinal trunk. From near each mesal angle of each longitudinal trunk a branch extends mesad where it ramifies amongst the viscera in order to aerate the digestive and reproductive systems. The cephalic portion of each trunk ramifies in the head and aerates the ganglia, antennæ, etc.

The *ventral tracheal system* is similar to the dorsal in that it possesses the same branches and ramifications in the abdomen with the exception of the ventral arch opposite the caudal pair of spiracles. This is replaced by the ramifying caudal extremities of the longitudinal trunks. The tracheæ of the thorax are quite different from those of the dorsal system. The first abdominal spiracle and that of the metathorax on each side are united almost directly by a somewhat curved trachea possessing a mesal branch which passes to the hind leg, and the two thoracic spiracles are united by a longitudinal trunk similar to that of the dorsal system, but which has a median mesal branch passing to the middle leg. There are two ventral arches, one uniting the prothoracic spiracles and the other those of the metathorax. Each of these arches possesses two caudal branches which ramify in the middle of the thorax, and cephalic branches from them may be observed. The cephalic branch from the anterior arch sends on each side a small trachea to each foreleg. In the prothorax the extremity of each lateral trunk bifurcates and ramifies in the head, in a manner somewhat similar to that of the corresponding dorsal trunks. (Pl. VII, *B*.)

In examining the oviparous female it will be seen that the system of tracheæ (Pl. XII, *B* and *C*) is very similar indeed to that of the wingless viviparous female. The longitudinal trunks do not seem to be as regularly zigzag as in that form, nor are there as many small branches noticeable; otherwise the two are identical.

In the winged forms the most interesting feature is the tracheæ of the wings about which the veins form. If an early wing pad is examined, tracheæ will be seen leaving the main trunk, as represented in Plate IV, *J*. It will be noted that what undoubtedly represents the median vein is forked once. One would naturally suppose these to represent M_{1+2} and M_{3+4}. Plate IV, *G*, shows one wing pad of an early pupa which the writer happened to find. The tracheæ in that instance were represented as there drawn. It will be noted that the media in this figure consists of four branches, and this would possibly seem to indicate that the veins as remaining represent M_1 and M_4. These veins certainly form in the course taken by those tracheæ in this one instance. In other examples, where only two branches are seen, these are in the same position. The tracheal system of the male has not been studied, but undoubtedly it is very similar to that of the wingless females.

Respiration is effected by means of the dorso-ventral muscles and the muscles of the spiracles, the contracting and relaxing of which depresses the body, or allows it to assume its normal position. This expels the air, or allows it to enter at the spiracles.

NERVOUS SYSTEM.

The work of Davidson (1913) upon the wingless form of this species does not agree exactly with our slides and dissections. His figures of sections agree with ours, but they are differently interpreted in regard to the subœsophageal ganglion.

In the wingless viviparous female the brain is small, a dorsal view (Pl. XIV, *A*) showing it to be not much broader than the thoracic ganglionic mass. It is composed of a pair of rounded pear-shaped ganglia which are fused, but an indication of the double nature remains. The *optic lobes* (*OpL*) are small and the nerves to the eyes (*OpN*) very long, whereas in the winged forms these lobes are large and their nerves extremely short. The *antennal nerves* (*AntN*) are given off from the antero-dorsal part of the *supraœsophageal ganglia*. The commissures connecting the brain with the *subœsophageal ganglia* (*SubOG*) are distinct and rather long, whereas those connecting the latter with the *thoracic ganglia* (*ThorG*) are very short. In fact the two masses, thoracic and subœsophageal, appear in some specimens to be entirely fused. The *thoracic ganglia* are fused into a large mass from the lateral margins of which nerves extend to the

legs. Each of these nerves becomes branched. From the caudal extremity of the thoracic ganglionic mass a narrow nerve cord extends caudad, and from this are given off numerous nerves, usually in pairs, one from each side. At its caudal extremity this *abdominal nerve cord* (*AbN*) is swollen into a *post-abdominal ganglion* (*PAbG*), from which nerves pass to the vagina and the posterior extremity.

In the sexual forms the nervous system is quite similar to that of the wingless viviparous female. The optic lobes, however, are larger, as will be seen by the figure of the male (Pl. XII, *J*).

In the winged individuals the ganglia of the head are somewhat different in form from those of the wingless ones, owing to the large optic lobes. As will be seen in Plate XIV, *B* and *C*, there are two large round optic lobes which form the lateral part of the brain. These are attached to a pair of pyriform-fused ganglia which in lateral view appear somewhat elongate. The narrowed distal extremity of this pair of ganglia passes downward and caudad toward the labrum. Here the pair separates for the passing of the pharynx, but is again united by the *commissure* (Com_3). From their lateral margins these two nerves extend downward and caudad and are in turn swollen into a pair of ganglia of the labrum. In some specimens these ganglia are very close together, almost united, while in others they are quite easily distinct. Situated just above commissure 3 and the pharynx is a pair of small ganglia not shown in the figures, which are almost fused and from which nerves extend upward and outward along the face of the large pyriform ganglia.

The subœsophageal ganglia are fused into a mass which is connected with the brain by two rather long commissures (Com_1). It is also almost fused with the thoracic ganglionic mass, though an indication of the commissures can be seen (Com_2).

The *compound eyes* are prominent in the winged forms, though absent in their more limited sense from the wingless ones. All wingless forms, however, have a small, tubercle-like eye composed of three lenses. These structures are found also in the winged forms at the caudal margin of the compound eyes proper, and are known as ocular tubercles. Each compound eye (Pl. XIV, *E*) consists of a large number of circular, slightly elevated, transparent structures separated from one another by a heavily chitinized portion of the integument. Each of these is a *cornea* (*Cor*), and directly beneath it is a goblet-shaped *crystalline lens* or *cone* (*Cone*). We are unable to make out any division in these lenses. From the proximal extremity of each lens a very fine *rhabdome* (*Rha*) extends to the basilar membrane. Each rhabdome is surrounded for nearly its entire length by an irregular mass containing *pigment* (*Pig*), which seems to have no very definite arrangement. The *basilar membrane* (*BM*) is easily distinguished. A section through the compound eye and optic tract

reveals just below the basilar membrane a very slightly swollen structure containing a few small cells. This seems to correspond to the *periopticon* (*POp*), though it is very small. Immediately below this is a bundle of fibers connecting it with the rather large lobe. This lobe contains two masses, apparently the *opticon* (*Op*) and *epiopticon* (*EOp*), which are situated quite closely together, separated by fibers and a few cells. Surrounding these two areas there is a mass of deeply staining large nucleated cells.

The *ocelli* are three in number and are present only in the winged forms. There is one median ocellus situated on the vertex and one situated anterior to each compound eye. Each ocellus (Pl. XIV, *O*) consists of a rather prominent rounded *lens* (*Lns*) from the base of which there extend inward a large number of fine fibers. These spread as they reach a disk-shaped structure and are here heavily pigmented, though no pigment is visible at their opposite ends at the base of the lens. Immediately behind the disk the fibers converge considerably to form the nerve which extends to the brain, but there is no pigment present in this portion.

SENSORIA.

Under the head of sensoria are grouped a number of structures, undoubtedly sensory, which are met with in the different forms. These are mostly located upon the antennæ, though occasionally they are found elsewhere. The most simple of these structures is a stout spine mounted on a tubercle (Pl. XIV, *I*), with which the antennæ of all forms are armed at their distal extremity. Of somewhat the same nature also are the rows of minute projections seen on the antennæ and which under a low power form the imbrications of the segments. These are arranged usually in irregular semicircles. The antennæ of the wingless forms are armed with *fringed sensoria.* These are more or less circular in form and are composed of an elevated ring or rim on the summit of which all around are located small tubercles. On each one of these tubercles a prominent hair is situated, which hairs form a fringe all around the structure. The fringed sensoria met with are of three forms: First, the simple fringed sensorium with the inside of the ring showing no peculiar characteristics. Such sensoria (Pl. XIV, *J*) are usually small and are located in groups near a more specialized and larger sensorium. Secondly, a fringed sensorium with a nipple (Pl. XIV, *H*). These organs are usually much larger than the simple ones, and the center of the ring is elevated into a nipple. This central elevation may be shallow or it may be very pronounced, as it usually is in the earlier instars. Thirdly, there is met with a fringed sensorium with the central portion formed into a prominent mushroom-like body (Pl. XIV, *G*). This central body is, in the young stages, where it is most prominent, a movable

structure, as it is so easily seen to be in some other species of Aphididæ.

On the antennæ of the winged forms a very characteristic structure is met with. This is the *transverse* or *annular sensorium*. On the underside of the segments extending usually about half way around the segment is a narrow, transverse, elevated ring. This, in rare instances, encircles the entire segment. The structure of these rings may be seen by examining Plate XIV, *K*. They consist of an elevated marginal part extending all about the organ, which, owing to its great length as compared to its width, appears like two elevations side by side with a membrane stretched between them. A transverse sensorium as seen in this species may be compared to a simple circular sensorium without fringe, which has been compressed on two sides until it has become very narrow and very elongate.

There are also upon the femora of the winged forms, and rarely upon the wing, structures which may have a sensory nature. These consist of small rings which inclose a transparent membrane and which are usually situated in an irregular, circular, transparent area (Pl. XIV, *M*).

The tip of the labium, also, is armed with a number of peglike sensoria (Pl. XIV, *L*).

OUTLINE OF LIFE HISTORY.

The life history of *Eriosoma lanigera* may be briefly outlined as follows: The egg is laid, as a rule, upon the bark of elm in crevices, though occasionally it is laid upon other trees. In the spring, toward the 1st of April, it hatches, and the young stem-mother so produced migrates to the base of a bud. Here she may remain for some days before the bud opens. Upon opening, the leaves curl or "rosette" about the insect, and in this house she produces her young. This second generation is wingless and lives within the curled leaves or upon the tender twigs. The generation matures late in April or in early May. It in turn produces a third generation, which is present upon the elm leaves from about May 1 until early June. An insect of this third generation is winged and is known as the spring migrant. It flies from the elm leaves to apple or related plants, settling upon the leaves, twigs, and water sprouts. Here it produces the fourth generation, which is wingless and which is the first generation on apple (Pl. XV, *B*) of the well-known woolly aphis. About July 1 this generation is mature and is giving birth to another generation (Pl. XV, *A*), the fifth, which is exactly like it. Many individuals of this fifth generation migrate to the roots, but others remain upon the twigs. Those which remain above ground produce a generation of winged forms, the sixth generation, which is mature about the middle of September. These fall migrants may be found

upon the trees until late autumn, but they nearly all migrate to the elms. Here they settle upon the bark and produce the sexual forms, males and females, small, wingless, beakless individuals. These mate, and the female, known as the oviparous female, then deposits her solitary egg in a crevice of the bark, where it passes the winter, to hatch as a stem-mother the following spring.

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PLATE II.

Banks's figures of *Eriosoma lanigera* published in 1817.

Aphis lanigera
Francis Bauer del.

PLATE III.

Antennæ of elm-feeding species of *Eriosoma:* *A*, Distal segments of antenna of migrant of *fodiens*, ventral view; *B*, same, dorsal view; *C*, same, terminal segment; *D*, distal segments of migrant of *cratægi*, ventral view; *E*, same, dorsal view; *F*, distal segments of spring migrant of *ulmi*, ventral view; *G*, same, dorsal view; *H*, same, terminal segment; *I*, distal segments of migrant of *americana*, ventral view; *J*, same, dorsal view; *K*, same, terminal segment. All greatly enlarged. (Original.)

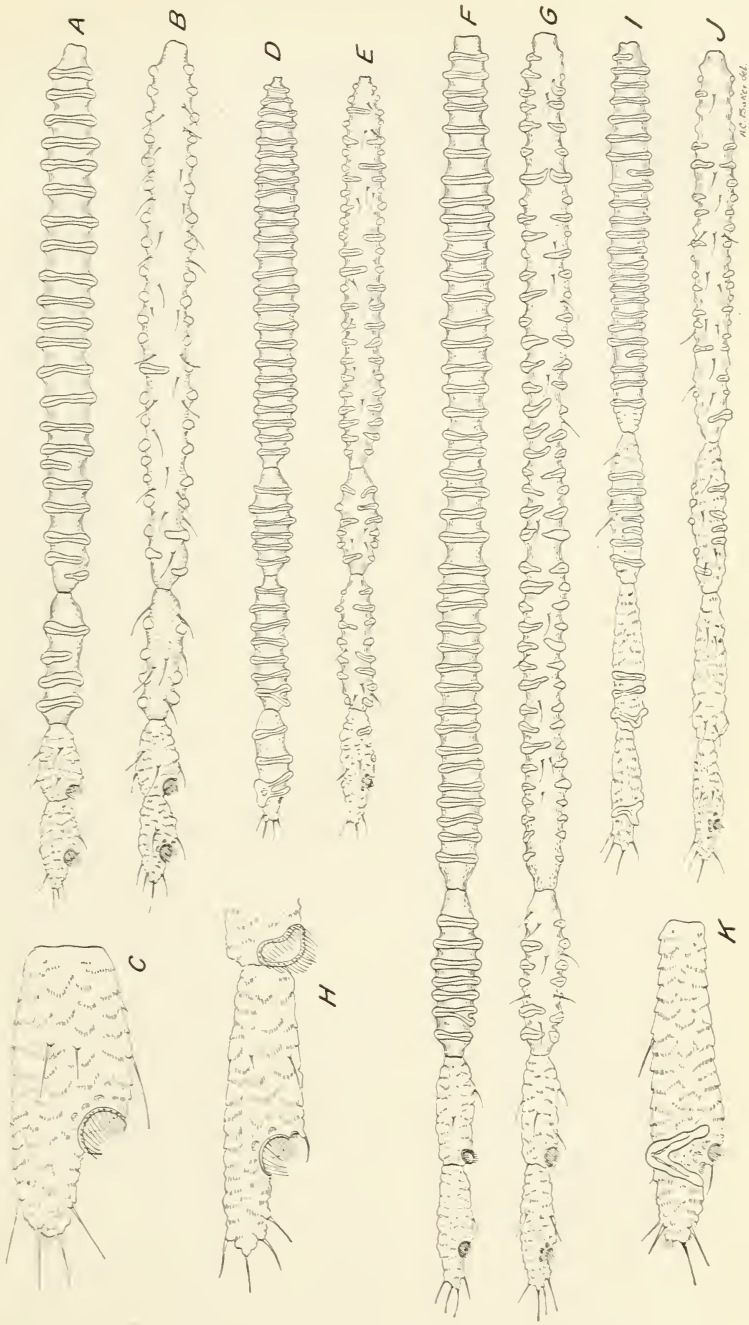
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PLATE IV.

Structures of *Eriosoma lanigera* and *E. americana: A*, forewing of *americana*, spring migrant taken June 1; *B*, forewing of *lanigera*, spring migrant taken on same date and tree as *A* and drawn to same scale; *C*, *E*, distal antennal segments of *americana*, spring migrant; *D*, *F*, distal segments of antenna of *lanigera*, spring migrant taken on same date as *C* and *E* and drawn to same scale; *G*, early wing pad of fall migrant of *lanigera*, showing tracheæ; *H*, freshly emerged forewing of spring migrant of *lanigera*, showing tracheæ; *I*, forewing of fall migrant of *lanigera; J*, wing pad of spring migrant of *lanigera*, showing tracheæ; *K*, hind wing of fall migrant of *lanigera; L*, spiracle, showing chitinized triangular region (*Ch*), orifice (*Or*), and margin of abdomen (*Mab*); *M*, internal structure of same, showing chitinized tube (*T*), tracheæ (*Tr*), and chitinized pieces (*a* and *b*). All greatly enlarged. (Original.)

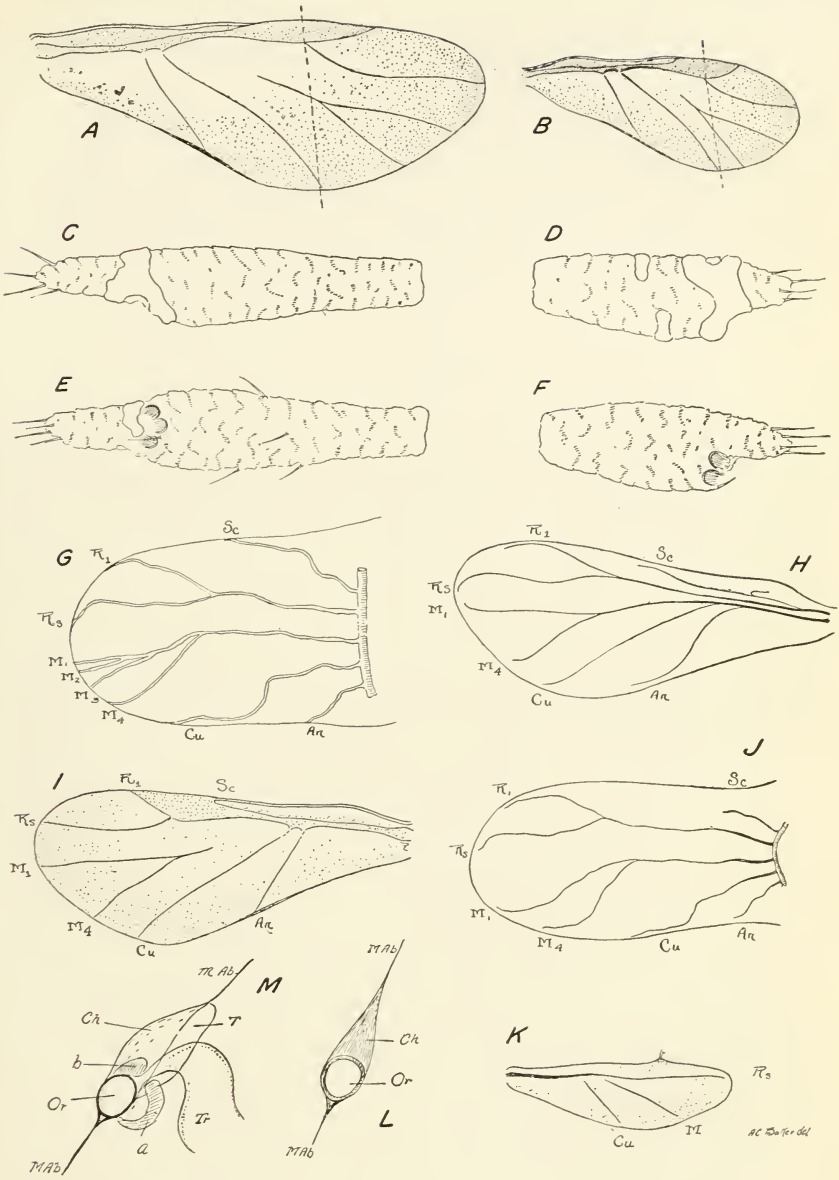
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PLATE V.

Structure of the skeleton of *Eriosoma lanigera: A*, Endoskeleton of head, showing transverse bar (*TB*), anterior ventral rod (*Ant VR*), ventral rod (*VR*), anterior dorsal rod (*ADR*), mandibular rod (*MandR*), maxillary rod (*MaxR*), dorso-lateral rod (*DLR*); *B*, foot of wingless viviparous female, ventral view; *C*, same, lateral view; *D*, endoskeleton of sternal plate; *E*, caudal apophysis; *F*, median apophysis, caudal view; *G*, median apophysis, lateral view; *H*, apodemes; *I*, foot of second instar wingless viviparous female, showing digitules; *J*, posterior phragma; *K*, hamuli; *L*, dorsal view of mesothorax (*MT*), præscutum (*Ps*), scutum (*Sc*), scutellum (*Scl*), postscutellum (*PScl*), anterior phragma (*AP*); *M–Q*, antennæ of wingless viviparous female in the first to the fifth instars; *R*, anterior view of dorsal portion of thorax, showing præscutum (*Ps*), scutum (*Sc*), prothorax (*P*), and anterior phragma (*AP*). All greatly enlarged. (Original.)

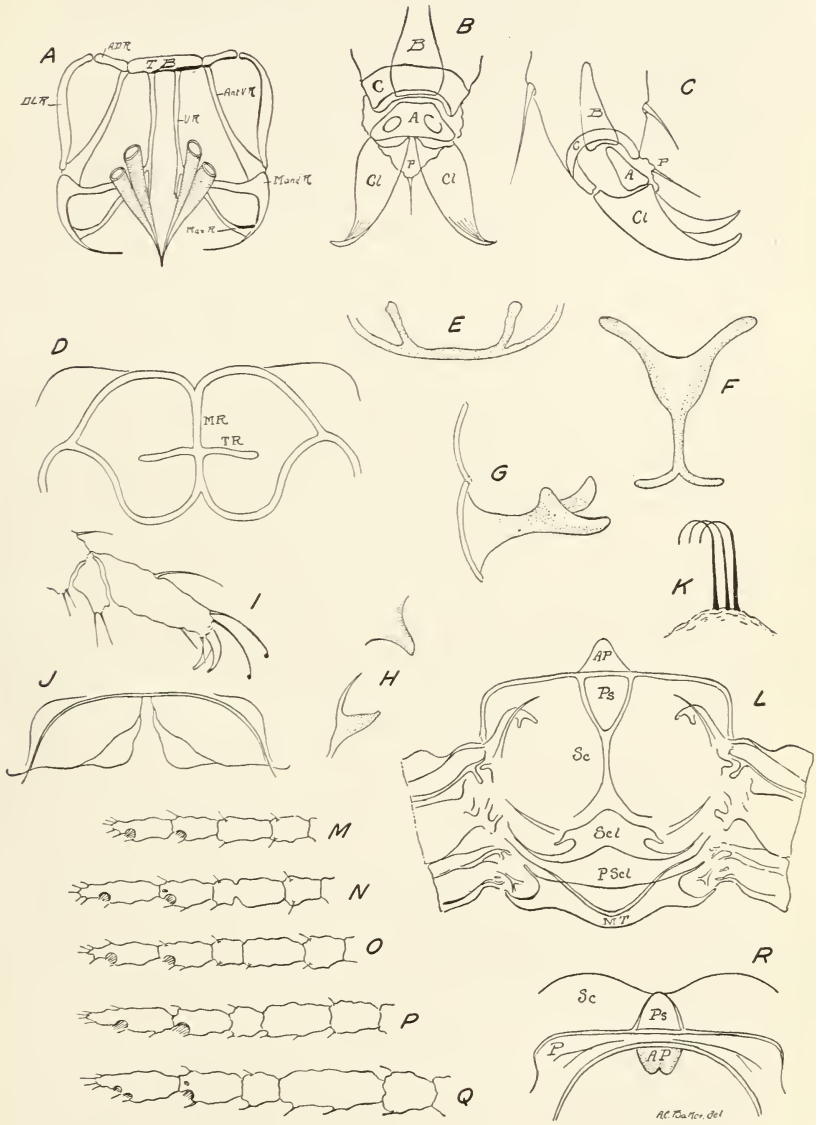
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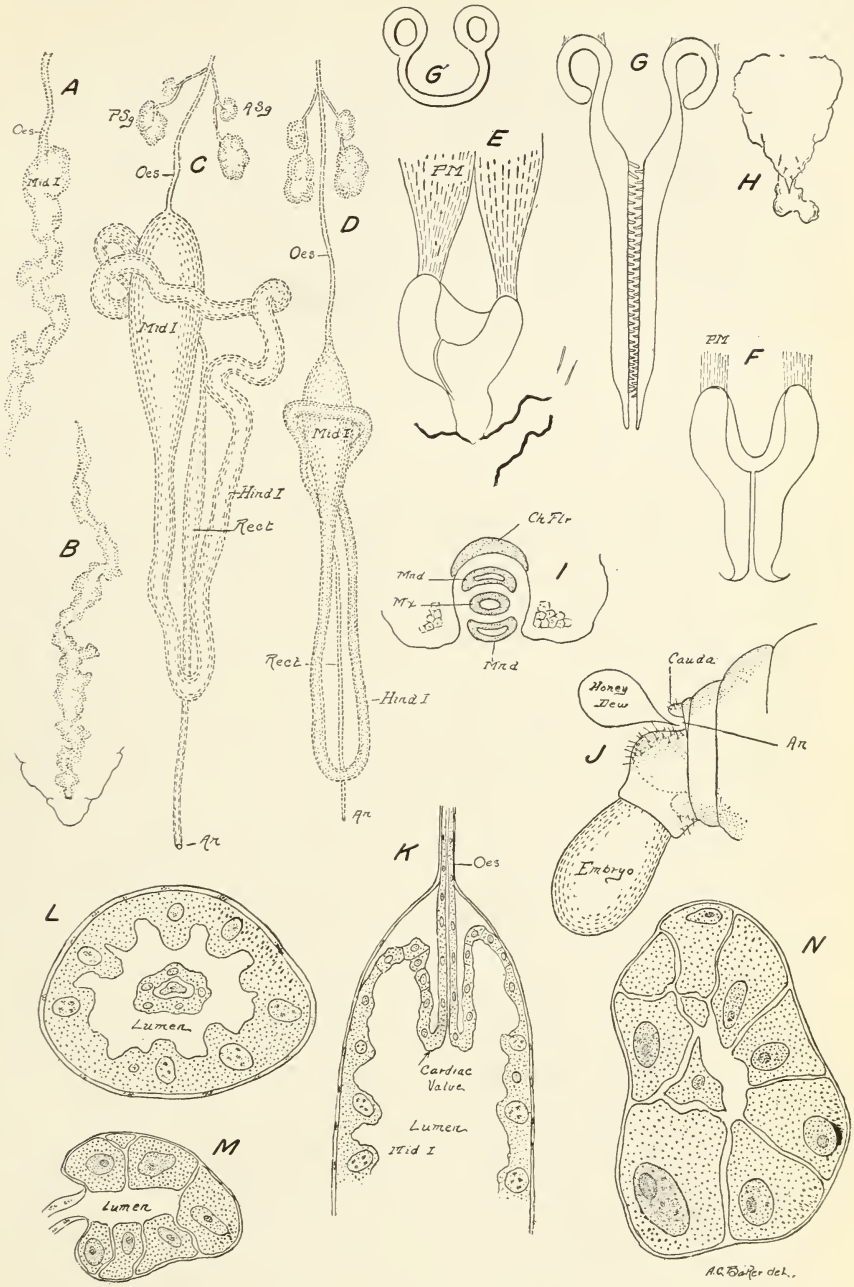
PLATE VI.

Digestive system of *Eriosoma lanigera: A*, Alimentary canal of male, first instar; *B*, alimentary canal of female; *C*, alimentary canal of stem-mother, showing anterior salivary gland (*ASg*), posterior salivary gland (*PSg*), œsophagus (*Oes*), mid-intestine (*MidI*), hind intestine (*HindI*), rectum (*Rect*), and anus (*An*); *D*, alimentary canal of spring pupa, second instar; *E*, salivary pump, as seen in paraffin section; *F*, diagram of salivary pump; *G*, pharyngeal pump of molted skin; *G′*, eye of same in life; *H*, trophic tubercle of female, showing rudimentary labium; *I*, transverse section of labium, showing mandible (*Mnd*), maxilla (*Mx*), and chitinized floor of the groove (*ChFlr*); *J*, caudal extremity of wingless viviparous female, lateral view; *K*, longitudinal section through cardiac valve; *L*, transverse section of mid-intestine in the same region; *M*, section of anterior salivary gland, showing duct; *N*, section through posterior salivary gland. All greatly enlarged. (Original.)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ASg
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Mid I
Hind I
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D
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Mid I
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An
G'
E
PM
G
H
PM
F
Ch Flr
Mnd
Mx
Mnd
I
Cauda
Honey Dew
An
J
Embryo
K
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Cardiac Valve
Lumen
Mid I
L
Lumen
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Lumen
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A.C. Baker del.

PLATE VII.

Dorsal and ventral tracheal, reproductive, and digestive systems of wingless viviparous female of *Eriosoma lanigera: A*, Dorsal tracheal system, showing dorsal trunk (*DT*), and dorsal arch (*DA*); *B*, ventral tracheal system, showing anterior ventral arch (*AVA*), posterior ventral arch (*PVA*), and ventral trunk (*VT*); *C*, spiracle; *D*, digestive system, showing oviduct (*Ovt*), ovarian tube (*OvT*), and chamber (*Ch*); *E*, digestive system, showing anterior salivary gland (*ASg*), posterior salivary gland (*PSg*), salivary duct (*SDt*), œsophagus (*Oes*), cardiac valve (*CardV*), mid-intestine (*MidI*), hind intestine (*HindI*), rectum (*Rect*), and anus (*An*). All greatly enlarged. (Original.)

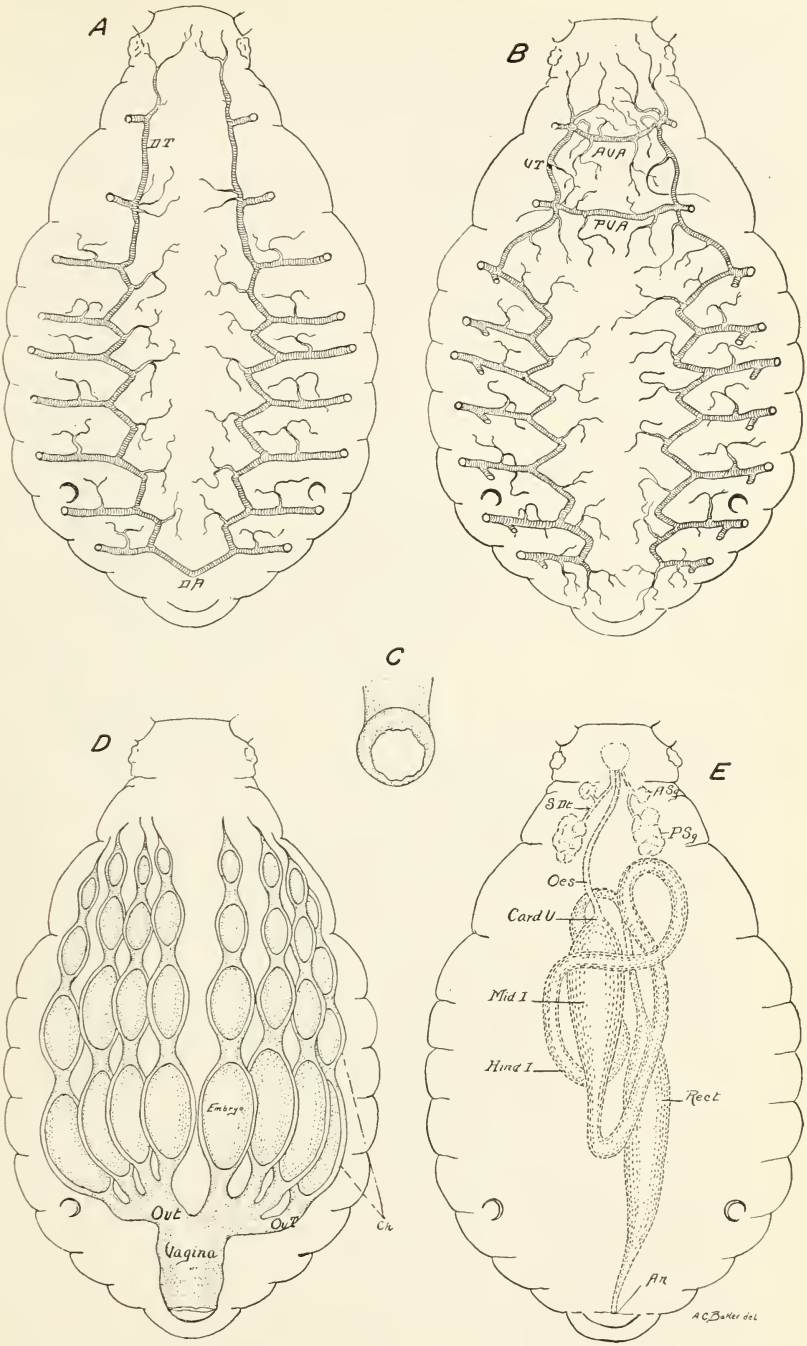
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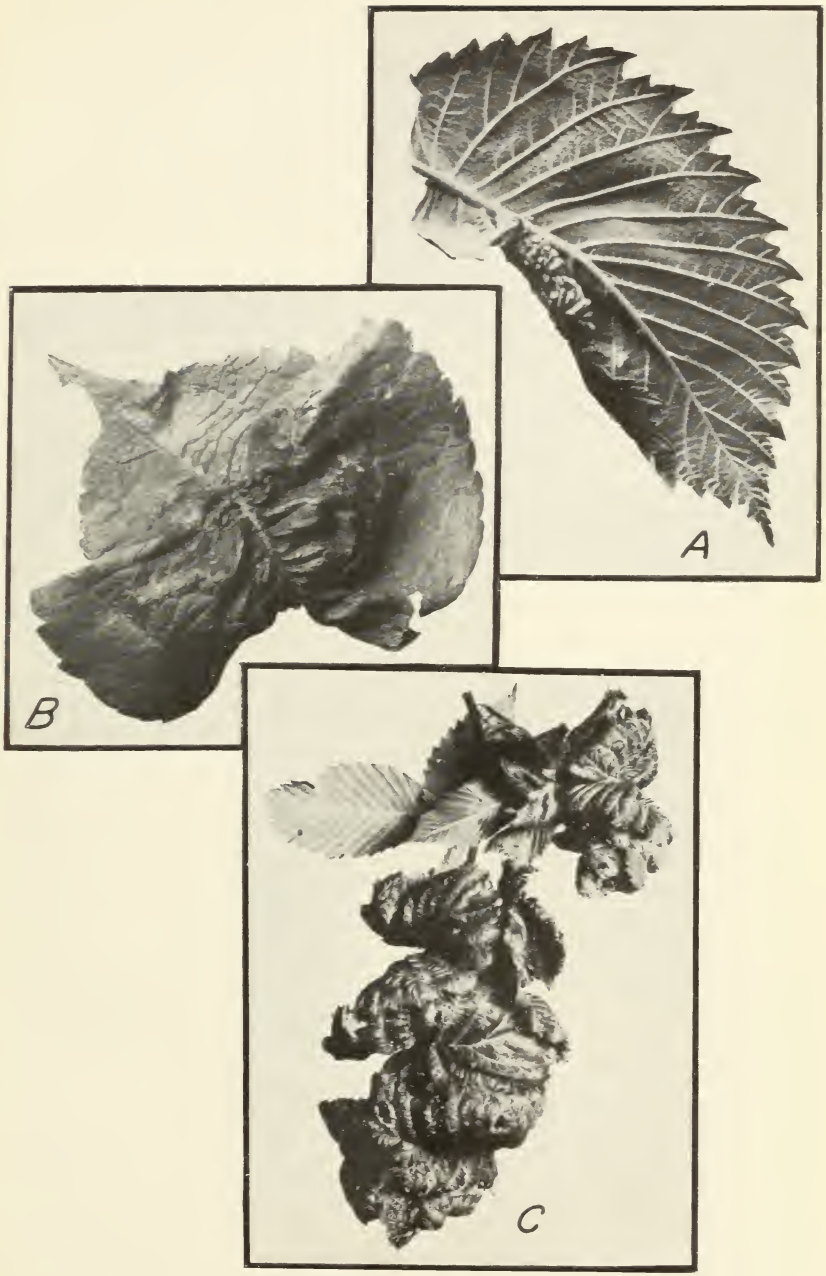
PLATE VIII.

Leaf galls of *Eriosoma: A*, Leaf of elm curled by *Eriosoma americana; B*, leaf of apple curled by *Eriosoma lanigera; C*, leaves of elm curled by *Eriosoma lanigera*. *A* and *B*, natural size; *C*, reduced. (Original.)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C

PLATE IX.

Galls of *Eriosoma lanigera* on apple: *A*, Root galls; *B*, twig galls. Natural size. (Original.)

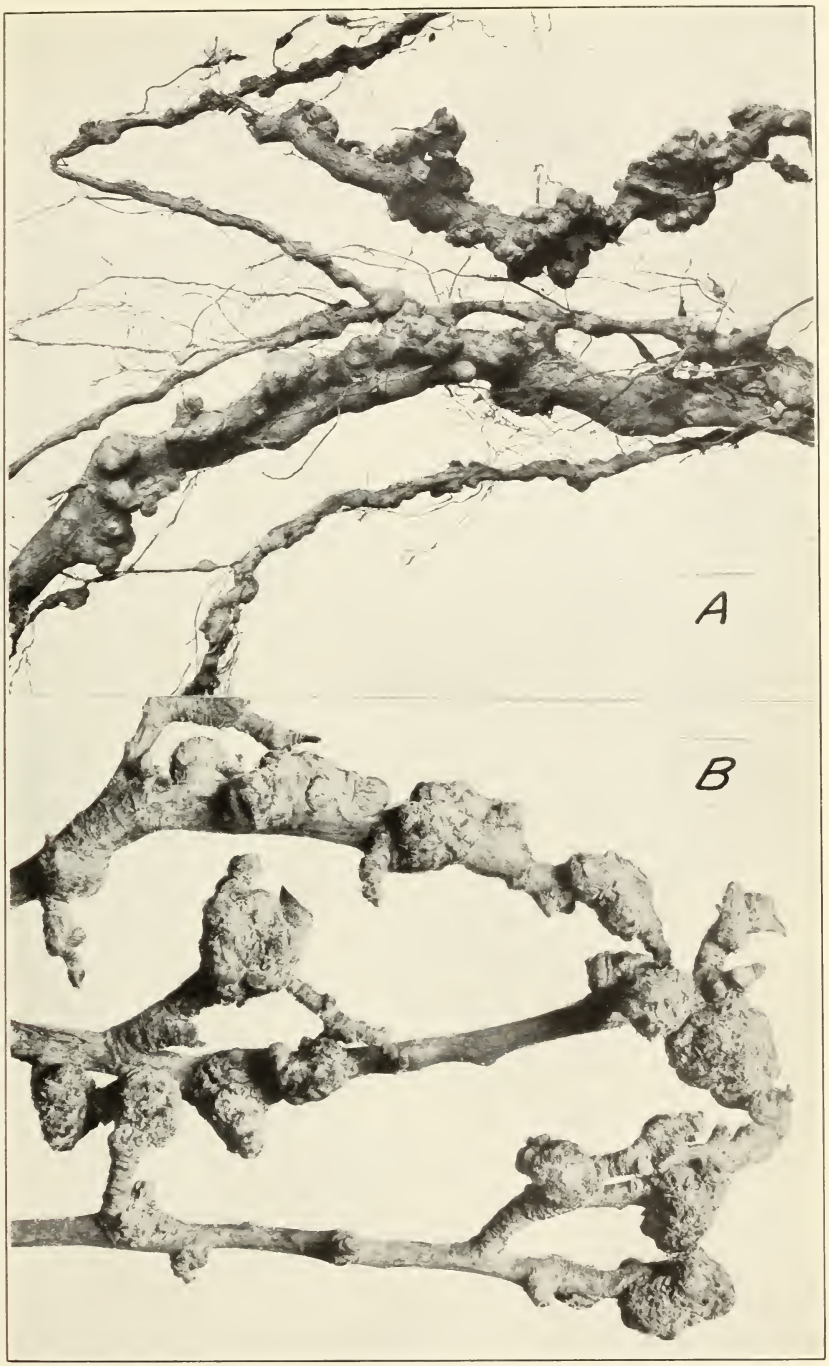
A
B

PLATE X.

Muscular system of *Eriosoma lanigera: A*, wingless viviparous female, showing elevators of antenna (*AntEl*), depressors of antenna (*AntDep*), depressors of head (*DepHead*), rostral muscles (*RM*), median longitudinal dorsal muscles (*MLDM*), median longitudinal ventral muscles (*MLVM*), lateral longitudinal dorsal muscles (*LLDM*), and lateral longitudinal ventral muscles (*LLVM*) (N. B. The longitudinal muscles shown are broader than the average; for normal width, see Plate XI, *K*. Dorsal muscles are shown on the right side, ventral muscles on the left side); *B*, muscles of coxa and trochanter, showing extensor of trochanter (*ExTr*) and flexor of trochanter (*FlxTr*); *C*, muscles of antenna, showing elevator of first segment (El_1), depressor of first segment (Dp_1), elevators of second segment (El_2), depressors of second segment (Dp_2), elevator of third segment (El_3), and depressor of third segment (Dp_3); *D*, transverse section through abdomen near distal extremity, showing dorso-ventral muscles (*DVM*); *E*, muscles of foreleg of wingless viviparous female, showing extensors of tibia (*ExTib*), flexors of tibia (*FlxTib*), extensor of tarsus (*ExTar*), flexor of tarsus (*FlxTar*), and tendon (*Tdn*); *F*, transverse section through thorax of pupa, showing large dorso-ventral muscles. All greatly enlarged. (Original.)

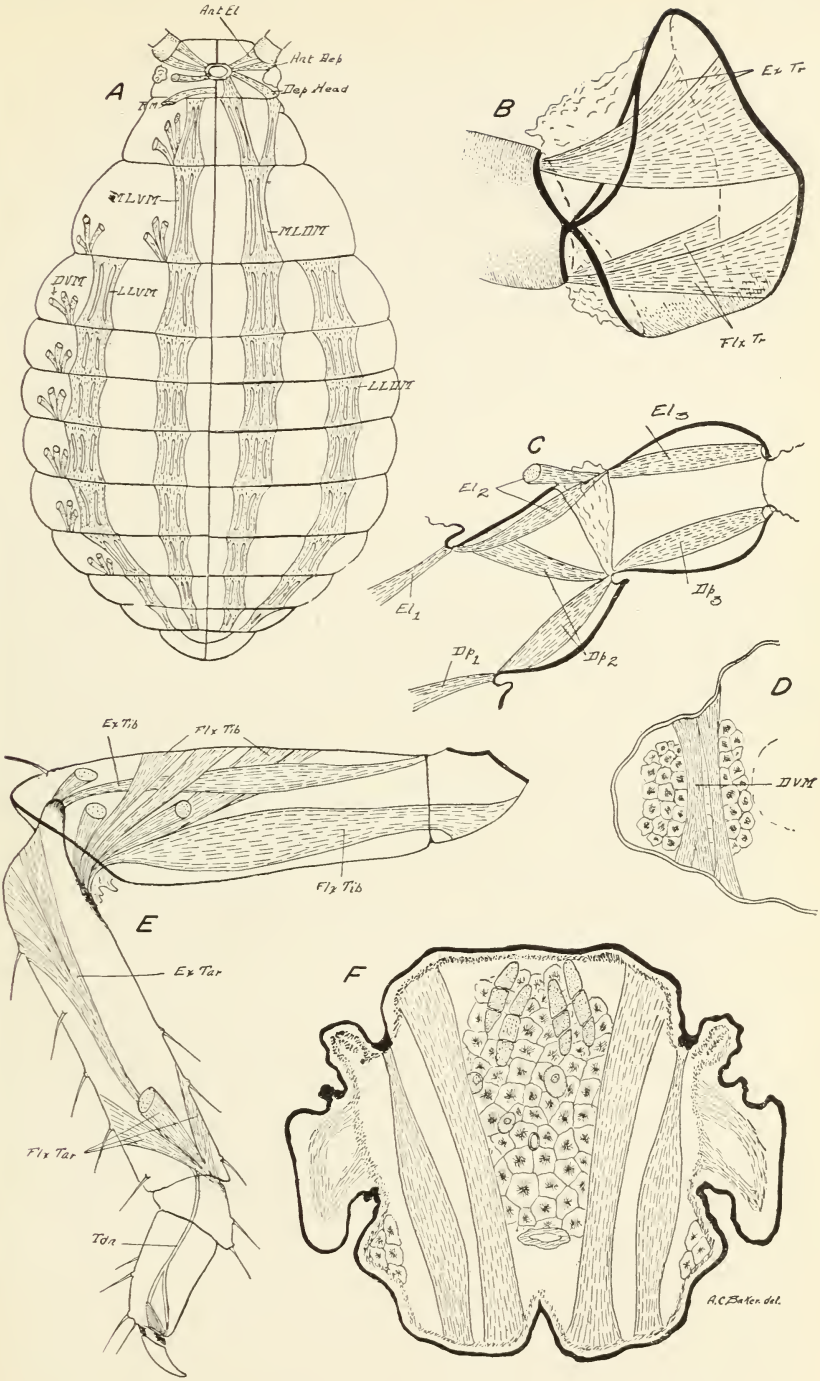
A
Ant El
Ant Dep
Dep Head
MLVM
MLDM
DVM
LLVM
LLDM
B
Ex Tr
Flx Tr
C
El3
El2
El1
Dp3
Dp1
Dp2
D
DVM
E
Ex Tib
Flx Tib
Flx Tib
Ex Tar
Flx Tar
Tdn
F
A.C.Baker. del.

PLATE XI.

Muscular system of *Eriosoma lanigera: A*, muscles of head, showing elevators of transverse bar (*ElTB*), depressors of transverse bar (*DpTB*), lateral pharyngeal muscles (*LPM*), pharynx (*Phar*), pump muscle (*PM*), salivary pump (*SalP*), salivary duct (*SalDct*), ganglion (*Gang*), clypeus (*Clyp*), labrum (*Lbrm*), labium (*Lbim*), and buccal cavity (*BucCav*); *B*, muscles of the setæ, showing retractors of maxillæ (*RMx*), retractors of mandibles (*RMd*), protractors of maxillæ (*PMx*), protractors of mandibles (*PMd*), maxillary setæ (*MxS*), and mandibulary setæ (*MdS*); *C*, setæ showing retorts (*R*); *D*, median apophysis, dorsal view, showing muscles; *E*, rostrum, showing muscles; *F*, longitudinal vertical section through thorax, showing dorsal and dorso-ventral muscles; *G*, median apophysis, caudal view; *H*, vertical longitudinal section of posterior phragma, showing attachment of muscles; *I*, median longitudinal dorsal muscles of thorax; *J*, lateral longitudinal dorsal muscles of thorax; *K*, pupa, showing, right half, ventral muscles, left half, dorsal muscles, elevators of antenna (*AntEl*), depressors of antenna (*AntDep*), rostral muscles (*RM*), muscle of cornicle (*CorM*), lateral longitudinal dorsal muscles (*LLDM*), lateral longitudinal ventral muscles, (*LLVM*), median longitudinal dorsal muscles (*MLDM*), median longitudinal ventral muscles (*MLVM*), dorso-ventral muscles (*DVM*); *L*, coxa, showing muscles which move it. All greatly enlarged. (Original.)

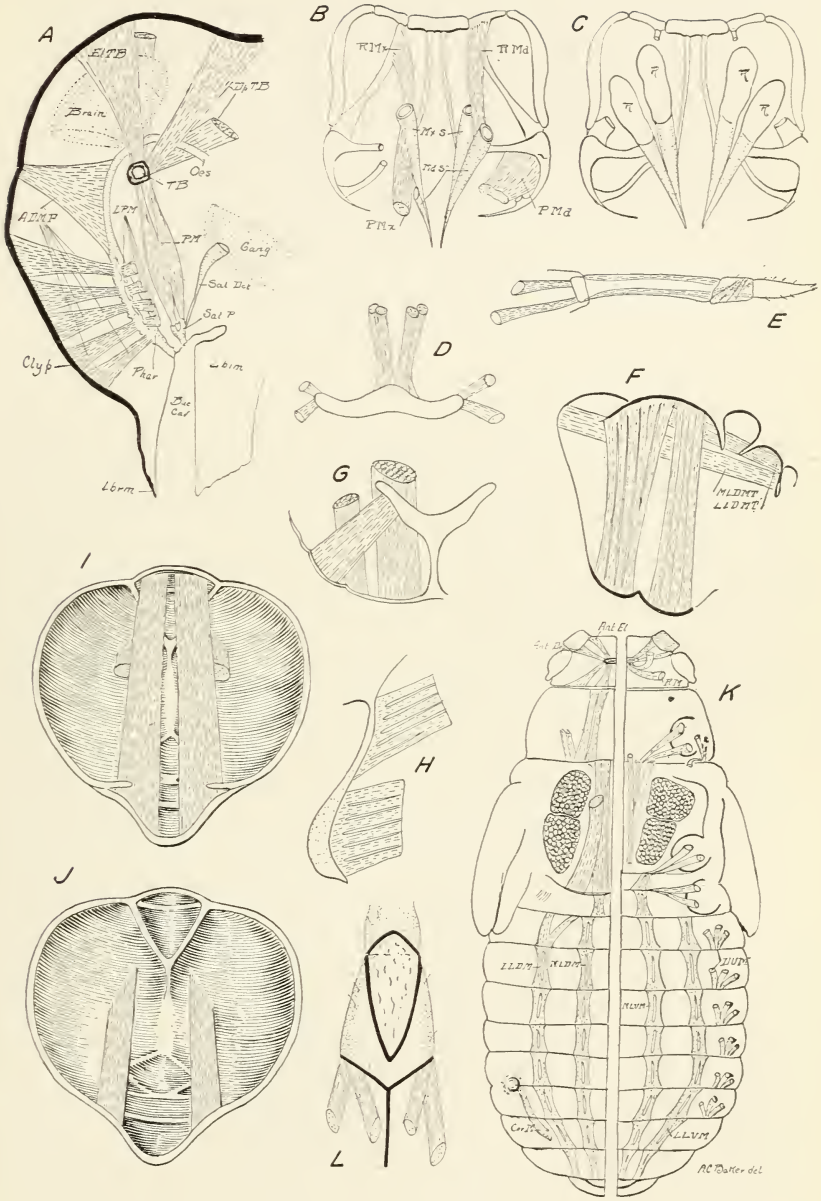
A
El TB
Dp TB
Brain
Oes
TB
ADMP
LPM
PM
Gang
Sal Dct
Sal P
Clyp
Phar
Lbim
Bac Cav
Lbrm
B
RMx
RMd
Mx S
Md S
PMx
PMd
C
E
D
F
MLDMT
LLDMT
G
I
H
J
L
K
Ant El
Ant Dct
RM
LLDM
MLDM
DUM
MLVM
LLVM
AC Batter del

PLATE XII.

Structures of sexual forms of *Eriosoma lanigera: A*, Oviparous female, showing egg within; *B*, oviparous female, ventral tracheal system; *C*, oviparous female, dorsal tracheal system; *D*, male genitalia, lateral view, showing penis (*P*) and claspers (*Cl*); *E*, male genitalia, ventral view; *F*, antenna of oviparous female; *G*, antenna of male; *H*, oviparous female, showing method of egg laying; *I*, oviparous female, reproductive system, showing gland (*Gd*); *J*, male, showing nervous and reproductive systems; *K*, male, reproductive system, showing testis (*Ts*), vas deferens (*Vd*), seminal vesicle (*S V*), gland (*Gd*), ejaculatory duct (*EjDct*); *L*, caudal extremity of oviparous female, showing cauda (*Ca*) and anal plate (*AnP*); *M*, transverse section through egg tube, showing egg within. All greatly enlarged. (Original.)

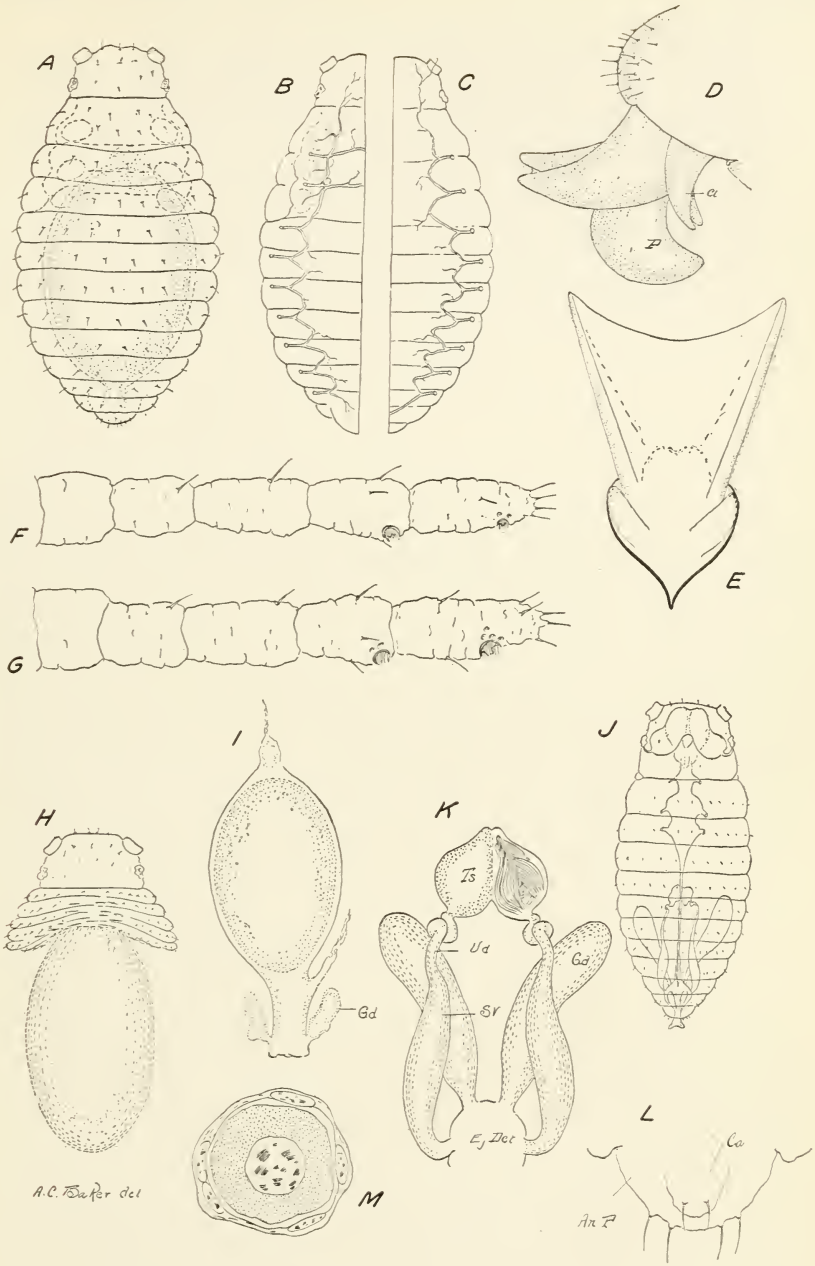
A
B
C
D
Cl
P
E
F
G
H
I
Gd
J
K
Ts
Ud
Gd
Sv
Ej Doc
L
Ca
An P
M
A.C. Baker del

PLATE XIII.

Wax-secreting structures of *Eriosoma lanigera:* *A*, Wingless viviparous female, showing location of wax pores; *B*, dissection of same to show wax reservoir and duct (*Dct*); *C*, surface view of wax pore of wingless viviparous female; *C′*, same of winged form; *D*, section of wax cell, showing chamber; *E*, cornicle; *F*, rim of cornicle from below, showing it nearly closed (*M*, muscle); *G*, same, open, showing orifice (*Or*); *H*, section through cornicle, wax duct, and wax reservoir, cornicle closed; *I*, same, cornicle open; *J*, caudal extremity of fall migrant, ventral view, showing genital plate (*GP*), and anal plate (*AP*); *K*, same, dorsal view, showing cauda (*Ca*); *L*, two distal segments of antenna of wingless viviparous female, showing sensoria. All greatly enlarged. (Original.)

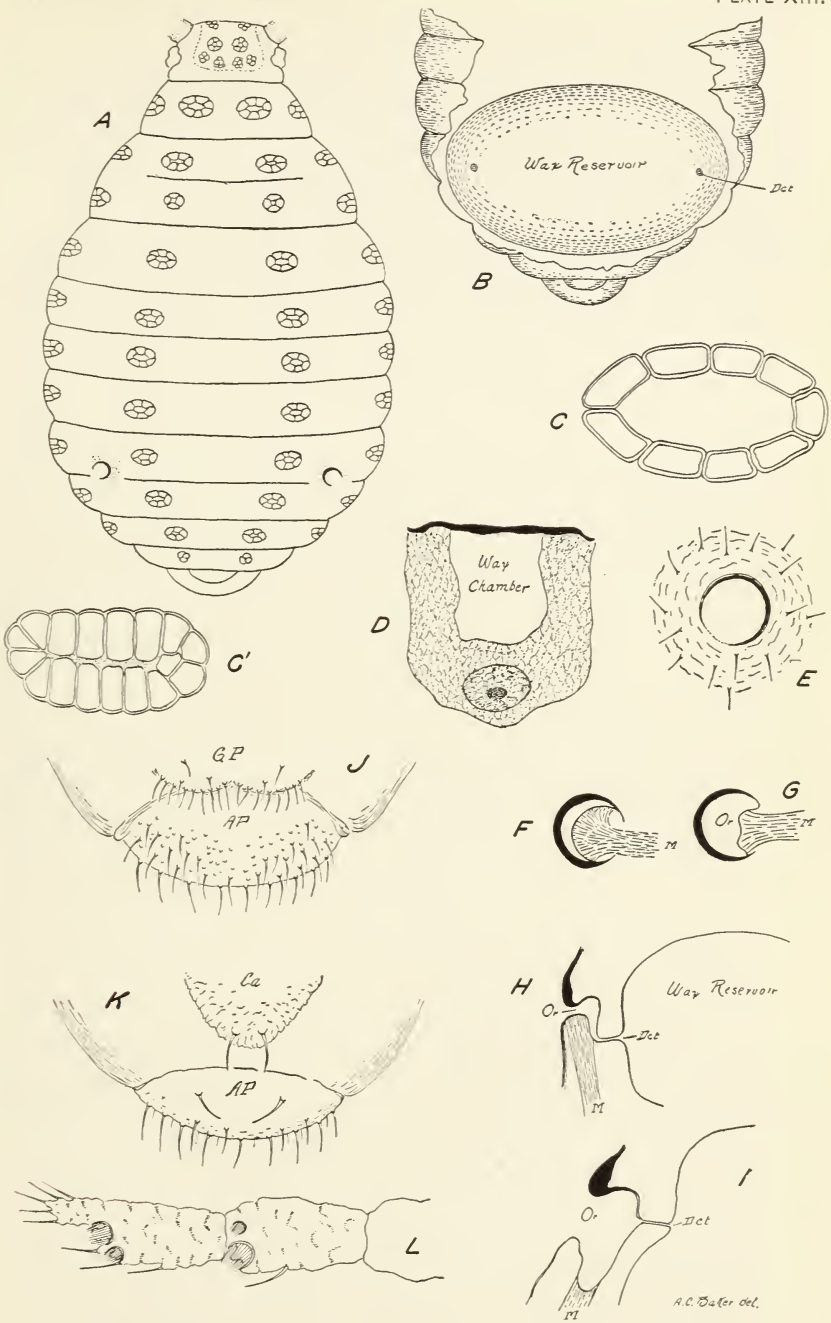
A
B
Wax Reservoir
Dct
C
C
C'
D
Way Chamber
E
GP
J
AP
F
M
G
Or
M
K
Ca
AP
H
Or
Wax Reservoir
Dct
M
I
Or
Dct
M
L
A.C. Baker del.

PLATE XIV.

Nervous structures of *Eriosoma lanigera: A*, nervous system of wingless viviparous female, showing antennal nerve (*AntN*), optic lobe (*OpL*), optic nerve (*OpN*), subœsophageal ganglion (*SubOG*), thoracic ganglion (*ThorG*), abdominal nerve (*AbN*), and postabdominal ganglion (*AbG*); *B*, brain of winged form, lateral view, lettering as in *1*, showing also circumœsophageal commissures (Com_1, Com_2, Com_3), and ganglion of labium (*LabGang*); *C*, same, ventral view; *D*, surface view of compound eye, showing cornea (*Cor*); *E*, section through optic tract and a portion of compound eye, showing cornea (*Cor*), cone (*Cone*), rhabdome (*Rha*), pigment (*Pig*), basilar membrane (*BM*), periopticon (*POp*), epiopticon (*EOp*), and opticon (*Op*); *F*, section through antennal nerve; *G*, fringed sensorium of antenna with central mushroomlike body; *H*, fringed sensorium of antenna with central cone; *I*, sensory spine of antenna; *J*, simple fringed sensorium; *K*, transverse sensorium of antenna of winged form, upper and lower view; *L*, sesoria on tip of labium; *M*, sensory structures on femur of winged forms; *N*, eye of wingless form; *O*, section through ocellus of winged form, showing lens (*Lns*); *P*, section through a seta and its retort; *Q*, transverse section through thoracic ganglion cutting one of the lateral nerves. All greatly enlarged. (Original.)

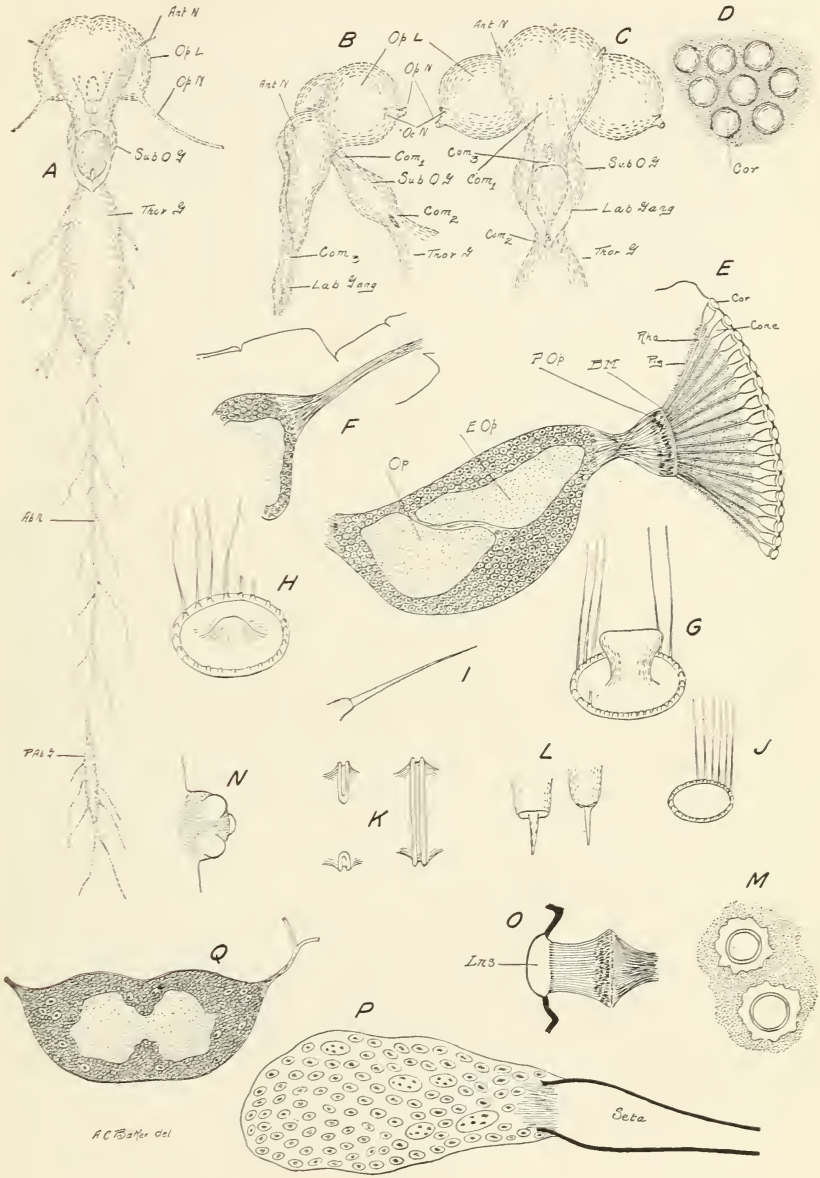
A
Ant N
Op L
Op N
Sub O G
Thor G
Abl
Pal G
B
Op L
Op N
Ant N
Oc N
Com 1
Sub O G
Com 2
Com 3
Thor G
Lab Gang
C
Ant N
Com 3
Com 1
Sub O G
Lab Gang
Com 2
Thor G
D
Cor
E
Cor
Cone
Rha
Pg
P Op
BM
E Op
Op
F
G
H
I
J
K
L
M
N
O
Lm 3
P
Seta
Q
A C Baker del

PLATE XV.

Aerial colonies of *Eriosoma lanigera* on apple: *A*, Summer generations of *Eriosoma lanigera; B*, colony of fourth generation of *Eriosoma lanigera*, the first generation on apple. Natural size. (Original.)

A
B